THE NUTRITIONAL BIOLOGY OF PERNA CANALICULUS WITH SPECIAL REFERENCE TO INTENSIVE MARICULTURE SYSTEMS

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Abstract

Field and laboratory studies were designed to identify nutritional and other factors affecting the feeding and growth of *Perna canaliculus* within mariculture systems in the Marlborough Sounds.

Field data was collected from mussel farms in Marlborough, and analysed to reveal how environment, community structure, feeding and growth varied between embayments, between farms and within mussel farms.

In the absence of adequate seawater flow through farms, up to 60% reduction of food occurred due to retardation of flow by farm structures and grazing by mussels. Decreased food concentrations limited feeding, condition and growth by mussels living at downcurrent sites within farms. Whereas the presence of adjacent farms did not limit food or food uptake, the manipulation of stock densities and farm structures may enhance food availability and provide a key to enhanced productivity.

Average feeding rates varied markedly between embayments, and this variation may be related to food availability. Mussels at a seaward site (Richmond Bay) had an even and low condition index whereas those in Crail Bay had a variable and high condition index.

Multiple regression analyses indicated that spatio-temporal changes in mussel length, temperature and food resources could explain the marked differences in feeding rates. Filtration rate was high or maximal below a food concentration of 1.5 ug l^{-1} chlorophyll *a*, but declined markedly above this threshold when a maximal ration was ingested. Assimilation efficiency declined from 85% during winter to 75% in summer, and did not become limited when maximal volumes of food were eaten by *P. canaliculus*.

Laboratory studies were designed to test a range of factors (below) that may affect feeding in the field, or perturb feeding in experiments.

Presence of gametes caused an 81% decline in feeding. However, mussels filtered normally after spawning and in the absence of gametes. Filtration ceased for 4 hours after salinity was reduced from 34 to 25ppt, then recovered to rates similar to those recorded at 34ppt. Filtration rate also declined ten-fold as oxygen concentration declined from 5 to 1.5ppm. However, current speeds of 5-28 cm s^{-1} did not affect filtration.

After deprivation of food, feeding behaviour depended on food concentration. At 0.3 mgC l^{-1} food, starvation increased filtration slightly. At 1.5 mgC l^{-1} food, filtration rate fluctuated markedly until rates stabilised at 48% of the maximum recorded rate, 18 hours after food deprivation. Feeding and energy budgets were therefore determined during long-term (24 hour) experiments.

Five separate phases of feeding behaviour were identified as food concentration increased from 0.03 - 10.0 mgC l^{-1}, a range extending below that recorded in the mussel farms of Marlborough (0.4 - 4.0 mgC l^{-1} food). 1. Filtration rates increased to maxima at 0.3 mgC l^{-1}. 2. Filtration then declined to 70% of this maximal rate as food concentration increased to 0.6 mgC l^{-1}. 3. Uniform filtration occurred from 0.6 to 1.0 mgC l^{-1}. 4. From 1.0-1.4 mgC l^{-1}, filtration declined and a maximum ration was ingested. 5. Above 4.1 mgC l^{-1} food, mussels filtered at minimal rate, appeared to ingest a maximum ration, and rejected food in pseudofaeces. Whereas phases 1-5 of feeding occurred in 80mm length class mussels maintained at 18°C and in three size classes of mussels maintained at 15°C, only phases 1, 4 and 5 were recorded in 80mm length mussels maintained at 12°C. Gut passage time increased below 15°C. Temperature may therefore affect both feeding behaviour and dietary regulation in *P. canaliculus*.

Mussels assimilated from 81% to 89% organic matter from *Isochrysis galbana*. Digestion was not affected markedly by changes in ingestion rate, temperature or mussel size. Thus, Growth Potential increased with food concentration to maximal values of 3.7-5.8% body C d^{-1}. Energy budgets indicated that growth rate increased with food concentration during phases 1-3 of feeding, but was independent of food during phases 4-5 of feeding. Whereas maximum Growth Potential increased with temperature, it was not dependent on mussel length within the range 30-80mm.

Comparison of field observations with results of laboratory studies indicated that feeding phases 3, 4 and 5 occurred in both situations. Thus, feeding only became severely food limited when food concentration declined markedly. However, only 0.5% of food consumed within farms was produced *in situ*, and adequate water movement in embayments and through farms was therefore needed to provide cultivated mussels with food. The structure of the cultivation system may constrain growth by mussels. In particular, the mussels' distribution within farms, and the distribution of farms between embayments limited production. Further understanding of the biological base of this industry may therefore enhance profit.

SECTION 1.

General Introduction

Initial interest in the commercial cultivation of the green lipped mussel, *Perna canaliculus* (Gmelin), arose due to declining stocks of benthic mussel communities (Tortell 1976). The mussel is an important member of the coastal fauna of New Zealand (Morton and Miller 1973) which has now been cultivated for over two decades. During the decade 1971 - 1980 mussel farming underwent rapid growth from a fledgling industry into the most productive form of aquaculture conducted in New Zealand. This expanding cultivation industry produced 10 759 tonnes of mussels in 1986 when exports alone earned NZ$12 million (Weeber 1987). Management of the industry is presently conducted using policies that attempt to resolve the conflicting interests of different water users; but these policies are formulated without an adequate knowledge of the nutritional and eco-physiological constraints which ultimately determine mussel growth. Consideration of these biological requirements could lead to an enhancement of the viability of the mussel mariculture industry.

The revenues generated by the industry are dependent on the weight of meat harvested from each farm. Meat weight is determined, in turn, by the size and condition of mussels at harvest. Any environmental or dietary constraint that retards somatic growth in *P. canaliculus* will also reduce the earnings accrued from mariculture operations.

Many factors may affect the growth and condition of *P. canaliculus* in intensive mariculture systems. The present study attempted to investigate the growth of mussels while monitoring both dietary and environmental factors.

There have been four previous studies in which the growth, reproductive cycles and condition of *P. canaliculus* have been investigated (Flaws 1975; Tortell 1976; Hickman 1979; Hickman and Illingworth 1980). These studies showed that tissue growth was affected by the gametogenic cycle. Flaws (1975) and Tortell (1976) showed that condition index declined markedly after mussels spawned at high temperatures (circa 18^{o}C). Shell growth also became reduced at both high temperatures and low salinity (Flaws 1975). Hickman and Illingworth (1980) also found that salinity and temperature were important and inferred that, in addition, food availability may have affected condition in the mussels that they sampled. However, none of the above studies determined either the food resource, diet or feeding of *P. canaliculus*.

It is therefore difficult to attribute the changes in growth and condition recorded during previous studies to food conditions or physico-chemical conditions occurring within the habitat. The present studies were conducted, in part, to fill this information

gap by investigating the nutrition of mussels within intensive mariculture systems while monitoring both dietary and other factors. In the absence of comparable studies on benthic communities of *P. canaliculus*, the present study may also provide the best indication available to date on how the mussel feeds in other, natural situations.

Mussel farming in New Zealand was originally conducted using raft cultures. Mussel farmers now employ a more sophisticated system using buoyed longlines to support mussels (Plate 1). The change to the new system occurred during the 1970's. Two concurrent studies (this study and Hickman, Waite, Illingworth and Meredyth-Young, in prep) represent the first detailed examinations of the factors affecting feeding (this study) and condition (Hickman et al; this study) within these more advanced aquaculture systems. My programme investigates the new relationships occurring between the development of mussels, and their nutrition and development.

Because more farms are distributed within a given area than before, and because each modern farm carries more stock than raft cultures, food factors may now be more critical to the growth of mussels. Thus, the impacts of the various parameters limiting growth by farmed mussels may now be different from those identified in previous studies. Also, different limiting factors may have become dominant in different locations. Therefore, the present study investigates the particular importance of location and environmental factors on the biology of *P. canaliculus*.

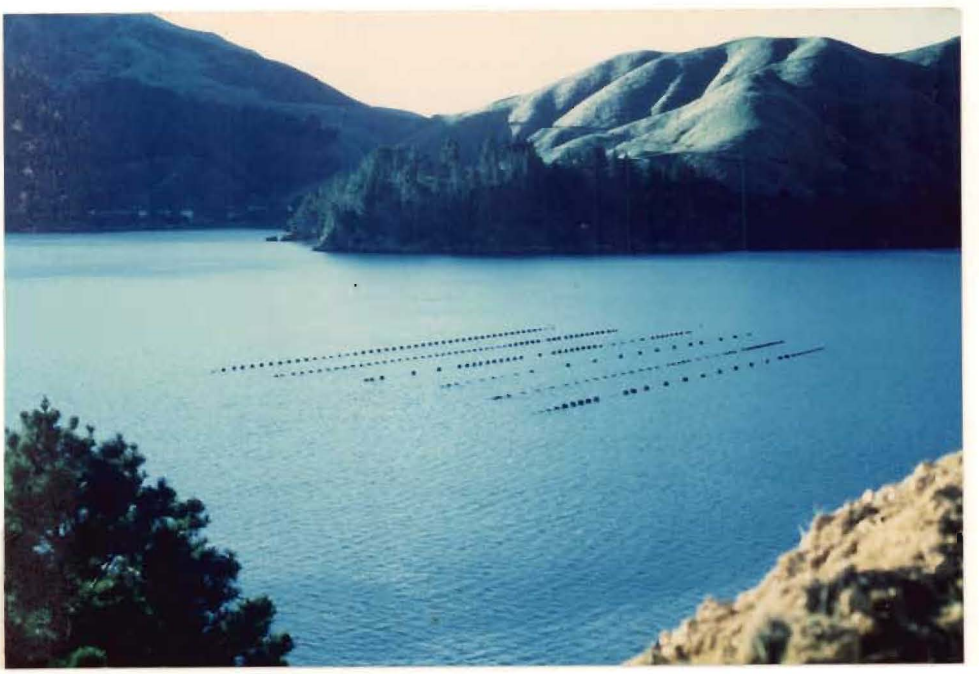

Plate 1. The layout of a typical mussel farm situated in Hallam Cove. Note that the six pairs of longlines are aligned parallel to the nearest shore.

The mussel farming industry was comprised of over 361 licensed farms in 1986 (Weeber 1987), most of which were located in the Marlborough Sounds. This area consists of a highly indented drowned valley system (Mackenzie et al. 1986), and farms are situated in these indentations or embayments. It is not known whether marked changes in the feeding or development of mussels occur between different embayments. Over 20 mussel farms have been sited in an embayment, and adjacent farms are often spaced only 300m apart. It is not known if feeding by these closely distributed mussel communities depletes the food concentration present within an embayment. A mussel farm typically comprises 5-10 pairs of longlines and covers an area of 3 hectares (Plate 1). Pairs of longlines are moored parallel to the shore and spaced 10-20m apart. The two longlines which comprise a pair are attached either end of buoys that both provide floatation and separate the longlines (Plate 2). A longline is 110m long and supports 220 culture ropes to which mussels are attached. Culture ropes hang vertically from 0 to 7m depth, and support up to 8 million mussels within a single farm (Plate 3). At the start of the present study it was not known whether feeding by the dense communities of mussels occurring in farms had reduced the food concentrations present, and thereby limited food uptake. Therefore, this study attempts to identify environmental factors that determine the diet and development of *P. canaliculus* under mariculture, and which can be managed to promote growth.

When my study commenced in 1983, little information was available on the nutrition of mussels grown within mariculture systems. There were no previous studies describing feeding by cultured mussels, and the flow of food and carbon through mussel farms had been described only for raft cultures of *Mytilus edulis* (Cabanas et al. 1979; Perez and Roman 1979). No information was available on the nutrition of mussels within longline culture systems similar to those utilised in New Zealand.

However, several factors have been shown to limit feeding and growth of *M. edulis* within natural, and other mariculture systems. For instance, if food is scarce then growth is retarded regardless of all other factors (Seed 1976; Robert et al. 1988). Food concentration is a primary determinant of the nutrition and growth of mussels (Stromgren and Cary 1984; Sprung 1985a,b; Page and Hubbard 1987). Up to 60% of food can be consumed within intensive cultures of *M. edulis* (Cabanas et al. 1979; Rosenberg and Loo 1983; Rodhouse et al. 1985), and such marked depletion of food may limit growth of mussels (Rosenberg and Loo 1983). It is important to determine whether food concentration also declines in mussel farms in New Zealand, and how the indigenous mussel *P. canaliculus* responds to reduction of food availability that may occur within local culture systems.

Nonetheless, the assumption that reduced food availability must result in reduced

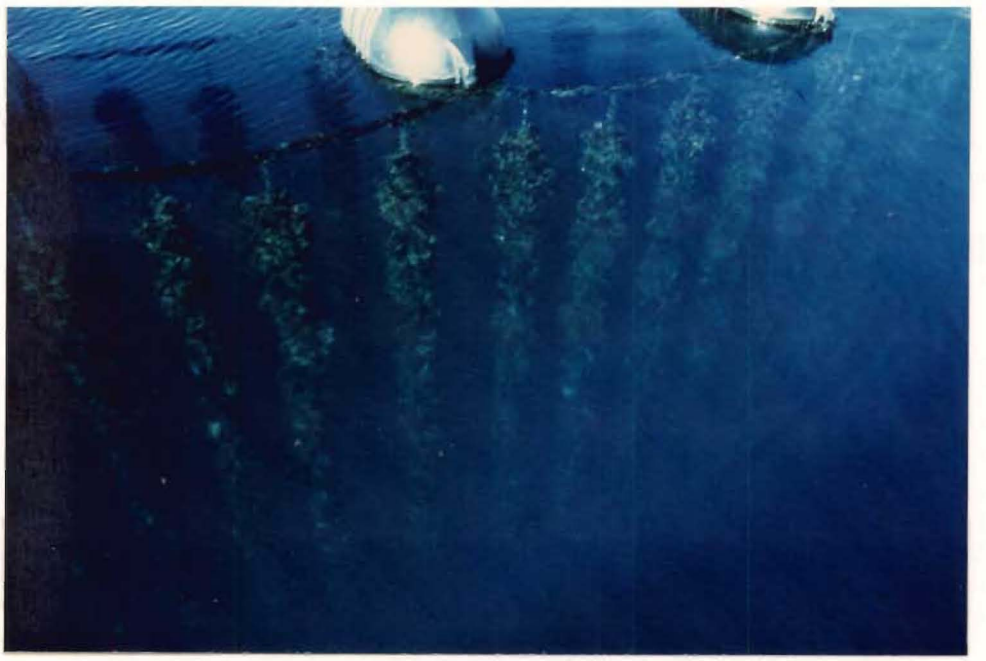

Plate 2. Mussels supported by the paired longline cultivation system. The far longline is spaced 0.8 metres from the nearest longline.

Plate 3. Mussels supported by a culture rope. Mussels are feeding, and have their exhalent apertures protruded.

growth may be simplistic. In extended experiments, *M. edulis* ingested maximal rations and grew at similar rates over extensive ranges of food concentrations (Winter 1973, 1978; Sprung 1984a,b). In addition, short-term studies suggest that although *M. edulis* consumed most food at high food concentrations, ingestion of excessive food can limit digestive efficiency and growth (Thompson and Bayne 1974; Bayne and Widdows 1978; Widdows 1978). Growth therefore does not necessarily decline with food concentration, and could perhaps be enhanced when concentrations of food are reduced from high levels. Research should therefore identify how *P. canaliculus* responds to reduced food availability.

After these short-term experiments were published both Riisgard and Randlov (1981), and Sprung (1984b) found that the feeding behaviour of *M. edulis* depended on the duration of the feeding experiment. Results from experiments on other species of mussel may also depend upon the duration of the experiment. Because the above changes in feeding behaviour may be linked to changes in food availability, the feeding of mussels may also depend on the consistency of food resources in the field.

Other factors (eg food type, temperature, mussel length) probably also affect the growth of mussels even when adequate food is present.

While *M. edulis* grew rapidly if the food resource contained marked proportions of phytoplankton (Incze et al. 1980), growth is limited by consumption of poor quality algal foods (Stromgren and Cary 1984). Whereas ingestion of silt may enhance digestive efficiency (Kiorboe et al. 1980, 1981), silt can also displace foods from the diet. The nature of ingested foods can therefore determine energy uptake and growth.

Optimal temperature regimes also exist. Filtration by *M. edulis* peaked at 16°C to 19°C (Wilson and Seed 1974; Schulte 1975; Sprung 1985b). Whereas growth was not dependent on temperature below 17°C (Page and Hubbard 1987), growth of *M. edulis* did decline markedly above 20°C (Incze et al. 1980).

Larger *M. edulis* had faster filtration rates (Winter 1973, 1978; Widdows 1978b; Sprung 1984b), resulting in faster removal of food from the water and a greater capacity for larger mussels to reduce food concentration and retard overall development within dense, crowded colonies (Frechette and Bourget 1985a,b). The size and spatial distribution of mussels within a colony therefore may affect the uptake of nutrients by mussels.

Sudden reduction of salinity caused feeding by *M. edulis* to cease for 2 days in experimental studies, and acclimation to unstable salinity regimes was not complete after 21 days (Widdows 1985). However, Lutz (1980) showed that in field conditions of 25-34 ppt *M. edulis* grew well. Salinity may therefore only inhibit development in certain estuarine habitats.

Current speeds below 5 cm s^{-1} did not affect feeding by *M. edulis* (Riisgard and

Mohlenberg 1979). However, faster currents inhibited both the feeding and growth of scallops (Wildish et al. 1987). As current speeds often exceed 5 cm s^{-1} in nature (this study), the affect of high current speeds on feeding needs to be investigated.

Many factors therefore need to be tested in order to identify the range of factors that limit the nutrition and growth of any species of mytilid and, having identified such a range, it is also of interest to determine the tolerance of each species to fluctuation of these factors. This tolerance range may indicate how mussels can adapt to different habitats, and how they respond to environmental changes which occur over different space and time scales within the culture system.

Ultimately, extensive investigation of the energetics of different species of mussels may also reveal how niche differentiation allows coexistence of different mussels. Unfortunately, little has been published on the feeding of species other than *M. edulis*. While changes in feeding occur with changes in food concentration and mussel length (eg *Aulacomya ater*: Griffiths and King 1979; *Choromytilus meridionalis*: Griffiths 1980; *M. chiliensis*: Navarro and Winter 1982; *Dreissena polymorpha*: Walz 1978; *Modiolus modiolus*: Winter 1969), these transitions were described using experiments of a single duration, and results should be extrapolated to different environmental situations with caution. The affect of other factors known to affect feeding and growth in *M. edulis* (above) is not known. Even less is known of the range of factors that affect the performance of the other species of mussels listed above. We therefore understand the nutritional biology of few species of mytilids, and are unable to predict how these mussels respond to changes that occur within their growth environment.

The present study attempts to investigate the feeding behaviour of *P. canaliculus*, and is designed to identify those constraints that limit diet and production in the field. One objective of this project was to derive and interpret nutritional data that may be used to improve the management of intensive mussel cultures. Results are therefore discussed with reference to the feeding of *P. canaliculus* within both natural and cultivated communities.

There is an urgent need to establish methods and criteria for the establishment of sub-lethal effects of environmental changes on marine organisms (Widdows 1978b). Feeding studies provide one suitable means of estimating the impact of environmental variation on mussels, but no ideal methodology has been established for the measurement of feeding in these important biological indicator organisms (below). During the present study, feeding was measured using both field and laboratory studies. Field measurements can provide accurate descriptions of feeding, show complex interactions between several environmental factors, and define the range of environmental change occurring in natural systems (Nicholajsen et al. 1984). However,

interaction between predictor variables reduces the ability of multivariate analyses to identify factors inducing change in dependent variables (Sokal and Rohlf 1981), and field studies may demonstrate variation in particular aspects of the mussel's biology without correctly indicating which variable or variables are responsible for such variation. In contrast, laboratory studies may show causal links between an artificial environment and feeding behaviour without establishing that such links actually occur in nature. Both types of investigation therefore may have inherent weaknesses that are not present in the other, and the two modes of study are considered complementary.

During the present study, both field and laboratory techniques are used to identify a range of factors associated with variation of feeding rates and condition in *P. canaliculus*. Field studies are described in Section 2, laboratory experiments are described in Section 3.

In Section 2.1 environment, feeding and growth of *P. canaliculus* were measured. In Section 2.2, preliminary identifications of causal relationships affecting the nutrition and development of mussels were made using multivariate statistical methods. In Section 3.1 a new, automated feeding system is then developed; the system is tested during studies of mussels reaction to the presence of spawn products. In Section 2.1 feeding by *P. canaliculus* is also examined at different current speeds, oxygen concentrations and salinities, and when exposed to food resources of differing abundance after starvation. In Section 3.2, filtration rates and energy budgets of the mussel are defined within two different experimental matrices. First, nutrition is studied within a mussel length - food concentration matrix (Section 3.2.1), then similar parameters are measured within a different water temperature - food concentration matrix (Section 3.2.2). Finally, in Section 4 the results of both field and laboratory studies are contrasted to determine whether feeding behaviours were similar in both studies, and some impacts of feeding by *P. canaliculus* upon its environment are discussed.

The above nutritional studies were conducted on *P. canaliculus* in pursuit of four primary objectives:

1) To identify locations where environmental factors may limit feeding and growth,
2) To define a range of factors limiting food uptake at different spatial scales,
3) To determine the mussel's feeding response to variation in each factor, and
4) To understand how mussels may feed over greater ranges of environment than occurred in Marlborough, and so attempt to predict growth in other systems.

SECTION 2.1.

Habitat, feeding and development of Perna canaliculus in intensive mariculture systems

ABSTRACT

Grazing by *P. canaliculus* was measured in seven mussel farms. Comparisons of hydrology, feeding and growth were made at three scales (between embayments, between farms in an embayment and within a farm). Marked changes in environment, gut content and condition occurred between embayments and within the boundaries of mussel farms, whereas little difference occurred between mussel farms in Crail Bay.

Marked depletion of food occurred within a farm, and was accentuated by the retardation of flow by farm structures. Up to 60% of available food was consumed as water moved through the farm, and faecal chloropigment was also reduced by up to 56%. Reduced food intake was associated with an 18% decline in tissue content of those mussels living in the centre of this farm in Crail Bay.

Presence of ten other mussel farms within an embayment (Crail Bay) did not cause any measurable reduction in the food available in the furthest downcurrent farm. Minor changes in faecal pigment that occurred between farms were not induced by the presence of other farms within Crail Bay. Mussel condition did not vary markedly between three farms located in Crail Bay.

The pattern of water flow through embayments was determined by tidal movements, wind and bathymetry; the form and position of embayments may affect the suitability of an embayment for aquaculture. Marked changes in food supply, salinity and temperature occurred between embayments, and these factors may have induced 1.5-7 fold variation in faecal pigment between embayments. Minimal faecal pigment occurred in mussels exposed to less than 1 ug l^{-1} phytoplankton chlorophyll during summer months, but faecal pigment content was not consistently low in any particular embayment. Averaged over all months, the condition index of mussels in Crail Bay (10.1%) was higher than in other bays (7.3-8.9%). Averaged over all sites, condition declined from 9.5% during winter to 6.9% in summer.

INTRODUCTION

Understanding how environmental factors affect feeding of mussels should be useful in deciding upon the positioning of mussels and mussel farms in optimal

environments that will allow mussels to grow quickly and achieve high condition.

Rapid environmental change can occur across boundaries separating different hydrological systems, and such changes can affect feeding and growth of bivalves (Navarro and Winter 1982; Sprung 1984a,b; Frechette and Bourget 1985b). During the present study, changes in environmental factors, and in feeding and growth of mussels was investigated at several locations in an important area of mussel cultivation. The study attempts to monitor maximal variation in feeding and growth by positioning sampling transects across possible boundaries between hydrological systems. Measurements were made at three scales (between embayments, between farms and within farms) at which changes in environment, feeding and growth may occur.

Variations in bathymetry (Lauder 1987) and hydrology (Flaws 1975, Tortell 1976; Heath 1982; Bradford and Chang 1987) occur between embayments in the Marlborough Sounds. A sequence of embayments was therefore sampled which extended from land locked sites to near the open sea.

Because mussel farmers have suggested that the presence of adjacent farms reduces food concentration and growth in their farms (J. Meredyth- Young, Pers Comm), a sequence of 11 farms in Crail Bay was sampled to determine whether food supply, and rates of feeding and growth varied between farms.

Reduced chlorophyll concentration has been reported in mussel farms in Europe (Cabanas et al. 1979; Rosenberg and Loo 1983; Rodhouse et al. 1985), and chlorophyll was measured as an indicator of food availability in 31 farms in 6 different embayments. Investigations were also made in a farm in Crail Bay to determine the impact of observed variations in food concentration within the farm on feeding and growth of mussels. Because alternating current direction prevented consistent reductions in food from occurring in any area of the farm, growth was also monitored in mussels that had been transplanted outside the farm to ascertain whether such changes in the availability of food had affected the mussel's biology.

This is the first investigation of feeding within mussel mariculture systems in New Zealand and, as such, the study attempted to determine at which of the scales listed above, changes in management practices could result in enhanced production of mussels.

METHODS

Unless otherwise stated, physico-chemical determinations and water samples were collected at a depth of 4 metres. Mussels were also collected from this depth. All sampling occurred between the 3rd and 13th of each month. Specific sampling dates are stated in Appendix I. All samples were collected during daylight (1100-1800), and at

[1] between different embayments,

[2] between farms within Crail Bay, and,

[3] within a mussel farm in Crail Bay.

Each embayment was sampled once every two months for one calendar year; all sites in Crail Bay were sampled once a month.

Samples Taken in Different Embayments

Live mussels were collected on farms in five embayments distributed along the Kenepuru and Pelorus Sounds (Fig 1). Samples were collected in Mills Bay (Site 1), Schnapper Point (Site 2), Four Fathom Bay (Site 3), Crail Bay (Site 4) and Richmond Bay

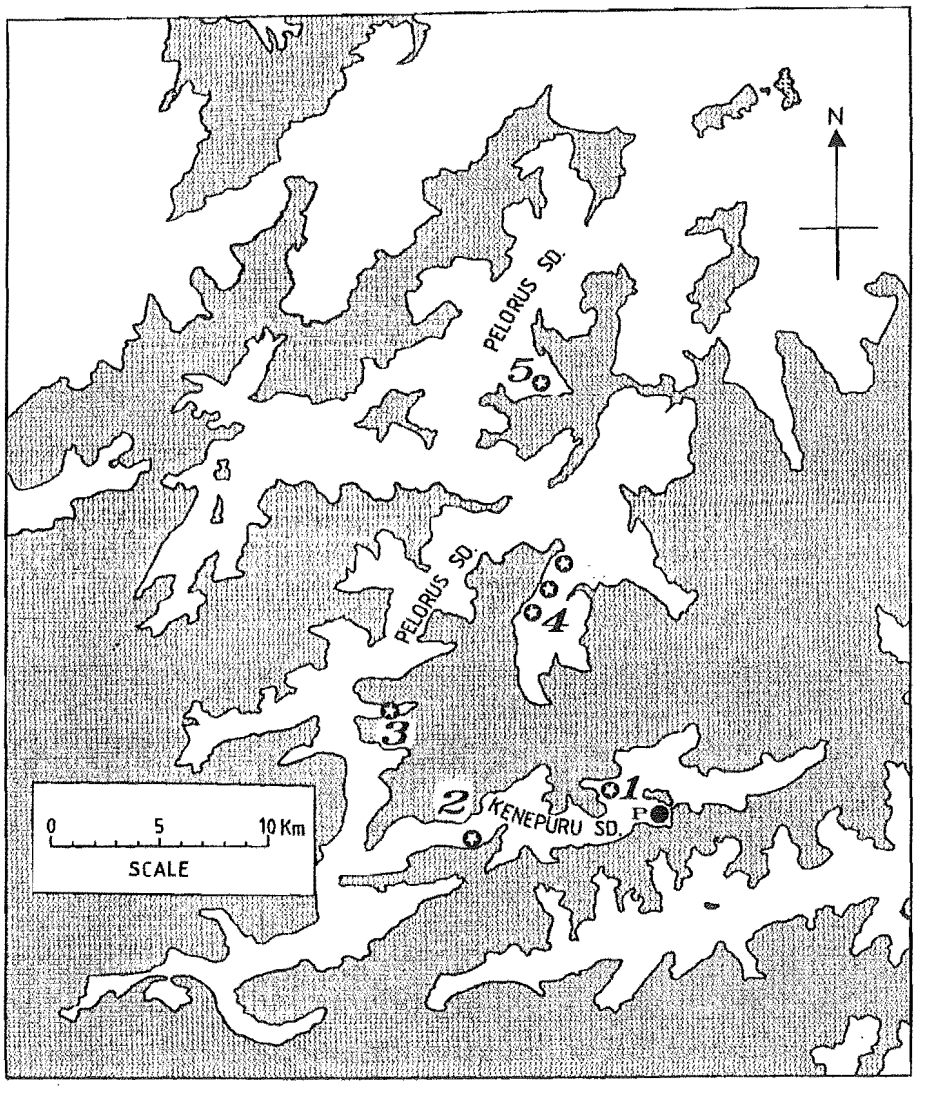

Figure 1. A map showing the location of principal study sites. 1:Mills Bay, 2:Schnapper Point, 3:Four Fathom Bay, 4:Crail Bay, 5:Richmond Bay, P:Portage Bay.

(Site 5). One embayment was generally sampled each day, and bays were sampled in the sequence Schnapper Point, Mills Bay, Four Fathom Bay, Crail Bay to Richmond Bay. This series of locations extended from land-locked waters of variable salinity and high turbidity, to seaward situations characterised by stable, high salinity and low turbidity. These differences were maintained by freshwater runoff entering the inner Pelorus and outer Kenepuru Sounds, and by the influx of seawater into the outer Pelorus Sound. The depth of water present at different sites also increased progressively from Mills Bay in the inner Kenepuru Sound (6m depth) through Schnapper Pt (11m), Four Fathom (13m) and Crail Bays (33m) to Richmond Bay (40m) located in the outer Pelorus Sound. However, the extent to which these differences in depth affect the movement of water and the transport of food is unknown. All sites were surrounded by high terrain which typically prevented high winds and heavy seas from prevailing at any of the sites sampled.

Samples of 28 mussels were collected at the upcurrent end of each mussel farm sampled. These sites were chosen because preliminary analysis of chlorophyll concentration indicated that food declined in many mussel farms. Mussels of both intermediate (25 - 60mm) and harvestable (60 - 110mm) length classes were collected from each embayment; each length class was comprised by a single cohort of mussels. Pigment content of faeces (ug chlorophyll equivalent), ash content of faeces (mg), length of individual mussels (mm), total and dry tissue weights (g) and condition index ([dry meat weight*100]/drained wet weight, %) were measured for each sample of mussels. This index of condition was used throughout the thesis as it provides an indicator of meat yield at harvest; the condition index used is therefore different from other indices reflecting the abundance of gonad tissues only. Chlorophyll concentration (ug l^{-1}), oxygen concentration (ppm), salinity (ppt), Secchi Disk transparency (m), temperature of seawater (^{o}C) and wave height (cm) were also measured in each bay. Turbidity was then determined as the reciprocal of Secchi Disk transparency (m^{-1}). Methods used to determine each parameter are detailed below.

Samples Taken from Different Mussel Farms in Crail Bay

Live mussels and seawater were collected from the upcurrent edges of three similarly managed farms positioned at the northern end, centre, and southern end of a linear sequence of eleven farms (Fig 2, p. 14) located in Crail Bay. Each farm contained 5-6 longlines that supported 6m length culture ropes spaced 0.5m apart. Sampling sites were located over 300m from the nearest upcurrent farm. Sampling sites were therefore spaced approximately 2.5km distant from each other. Only large mussels of harvestable size (60-110mm shell length) were taken from each farm. Otherwise, all determinations listed above were also made on samples collected from each farm.

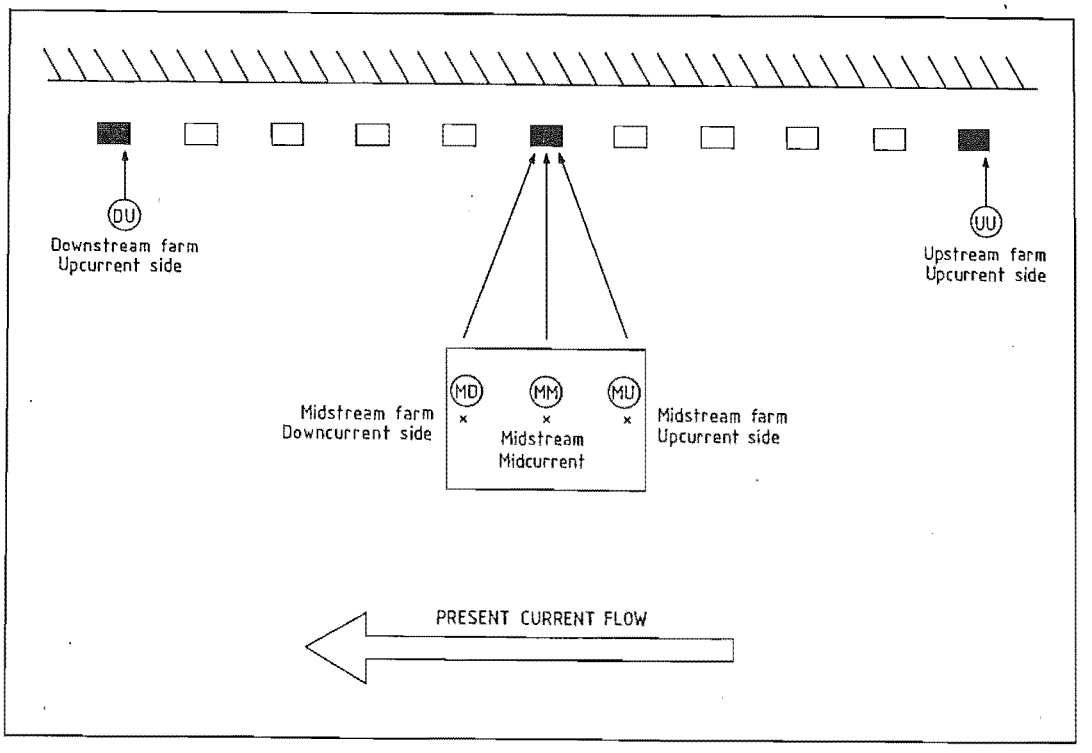

Figure 2. The spatial distribution of study sites in Crail Bay.

Samples Taken Within a Mussel Farm in Crail Bay

Water and mussel samples were also collected from the northern end, centre, and southern end of a single longline within a farm in Crail Bay (Fig 2). Again, only large, harvestable mussels (60-110mm length) were collected, and all measurements listed in (1) above were made.

Determination of Physical and Chemical Environmental Factors

On all sampling occasions, water samples were collected at 4 metres depth using a centrifugal pump. Each sample comprised by 5 l seawater was passed through 50 um mesh to remove large particles, eg. copepods, and then stored in the dark prior to analysis. Each measurement was repeated on three different 5 l water samples collected two hours apart.

Conductivity, oxygen concentration and temperature were determined at 4 m depth with a Horiba U-7 Water Checker. Secchi disk transparency was also recorded.

Two litres of seawater was passed through a 45mm diameter Whatman GF/C filter. These filters were then assayed for phytoplankton and particulate matter. Chlorophyll *a* and phaeophorbide *a* were determined from absorbance of extracts in 90% acetone measured both before and after acidification with 0.3 ml of 1 M HCl at wavelengths of 665 and 750nm (see Lorenzen 1967; Wilkinson 1983). Plankton pigment concentrations were determined using the following equations of Wilkinson (1983):

$$C = (E_a - E_b) * 27.31 (v/(V_f * L))$$

$$P = (46.43\ E_b - 27.31\ E_a) * (v/(V_f * L))$$

where C is chlorophyll *a* (ug l^{-1}), P is Phaeophorbide *a* (ug l^{-1}), E_a is the extracts absorbance at 665nm minus the absorbance at 750nm before acidification, E_b is the extracts absorbance at 665nm minus that at 750nm after acidification, v is the volume of 90% acetone used to extract the pigments (ml), V_f is the volume of water filtered (l) and L is the path length of the cuvette used (cm).

Particulate Organic Matter (POM), Particulate Inorganic Matter (PIM) and Total Particulate Matter (TPM) present on GF/C filters were assayed by weight. Particulate matter determinations were made on pre-weighed filters dried at 100°C for 24h, then weighed, ashed at 450°C and reweighed (see Strickland and Parsons 1968). The results obtained were corrected by comparison with blank pre-weighed filters that were processed in the same manner as filters through which seawater was passed.

Chloropigment and particulate matter data was also collected at 4 metres depth and at two hourly intervals by R.H. Hickman (MAFfish) who used identical methods. These data were used to describe foods present in different embayments. I completed these assays of foods from sites located in Crail Bay. Determinations of other hydrological factors were all conducted by myself.

At all sites, continuous profiles of chlorophyll *a* concentration ("*in vivo*" chlorophyll *a* concentration: Lorenzen 1966) were made at 4m depth. These showed changes in the abundance of phytoplankton along 550m transects extending between and through adjacent mussel farms. Fluorescence of chlorophyll *a* was measured using a Turner Designs 10-005 Fluorometer operated in flow through mode, and was adjusted against extracted chlorophyll *a* to correct for photoinhibition.

Water Movement

Three types of study were used to investigate flow near farmed mussels.

Flow velocities were measured at 1m intervals from 1-12m depth in farmed areas in Crail Bay (11/8/84) and at Schnapper Point (4-4-84 and 7/6/84). Both farms were selected because they contained longlines aligned parallel to long and relatively straight shorelines. Flow of seawater was measured using a hand-held Aanderaa Current Meter. In these two farms, stock hung at 0-6m depth from a pair of longlines attached at either end of a 0.8m long buoy. Two profiles were made. One was recorded between the paired longlines, the second recorded one metre away from the two paired longlines.

Four continuously recording current meters were moored around the central farm in the Crail Bay sequence from 4 August to 27 September. One meter was moored at a

depth of 3m and 50m off the offshore longline; a tide gauge was attached to this mooring. The second and third meters were set 1m off the middle of a longline supporting 100mm long mussels, and were positioned at 3 and 10m depth respectively. A fourth meter was moored at 3m depth, 1m off a longline carrying 40mm long mussels. Each meter recorded flow every ten minutes over a period of 47 days (raw data courtesy of NZ Oceanographic Institute). Daily observations of wind and sea state were made during this period from a meteorological station directly above the study site (data from NZ Meteorological Service).

Changes in flow between the flood and ebb tide were determined in Portage Bay (24-25 January 1984) when light NE winds (0-2 Beaufort) occurred. Rhodamine WT dye was released at 1 and 4m depth at the northern end of the bay at the start of both a flood tide and an ebb tide, and drogues were released at 1 and 4m depth at the same time. The positions of both drogues and dye markers were plotted every 30 minutes, and the rate of mixture of dye with seawater was measured with a Turner Designs 10-005 Fluorometer which had been zeroed on unfiltered seawater. Fluorescence of the 1m deep dye mass was measured on release, and again at the mouths of Portage Bay and Take In Bay. The fluorescence of the 4m dye mass was determined wherever upwelling brought this dye to the surface. Dilution was calculated by dividing Rhodamine concentration at point of release by the concentration determined at subsequent positions of the principal dye mass. Two separate dilution factors were calculated from (1) maximal and (2) mean dye concentrations recorded at each site.

Gut Content and Mussel Development

Gut contents of mussels were estimated using assays of faecal dry matter and faecal phytopigments. Preliminary investigation showed that inorganic matter was lost during the feeding process (Section 2.2), but that degradation of chloropigment probably did not occur. The sampling strategy was therefore optimised to reduce error in determining faecal pigment, the next most variable factor. A nested ANOVA indicated that sampling 28 mussels should provide estimates of faecal pigment with 95% confidence intervals of less than 20%, in 95% of cases determined.

At each site, 28 mussels were collected at 4m depth from a single culture rope. Growth densities (N m^{-1}) of mussels and visual estimates of packing density were recorded before mussels were cut from each rope. Each sample was scrubbed, and then divided into four equal replicates of seven mussels.

The four replicates of mussels were put into filtered seawater (aerated and typically maintained at ambient temperatures of 9-19^{o}C) in partitioned, cylindrical faecal collection chambers (190mm high and 200mm in diameter, Plate 1). Vertical perspex sheets interlocked at right angles, and two pairs of interlocking sheets were

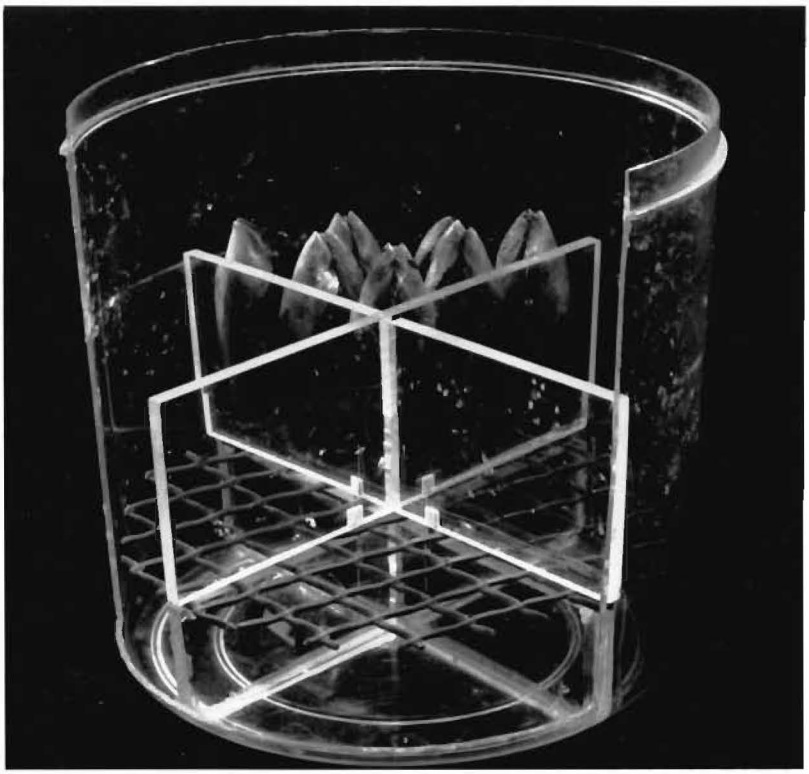

Plate 1. A faecal collection chamber, showing one group of seven large (87mm length) mussels supported on the mesh.

separated by a horizontal 20mm mesh plastic screen (bottom pair: 30mm high, top: 70mm high). The 4 groups of 7 mussels were supported on this mesh, through which faeces settled and could not be ingested by mussels. Defaecation was 95% complete in 24h, and faeces were collected after 36h and assayed for chloropigment, organic matter and ash content.

The faeces produced by each separate group of 7 mussels were suspended in 5ml distilled water and the total volume of each suspension was measured in a calibrated syringe. A 1ml aliquot of each suspension was assayed for chloropigment (after Wilkinson 1983). A second 1ml aliquot was also dried, weighed, ashed at 450^{o}C, and then reweighed to determine organic and ash content (Strickland and Parsons 1968). All remaining faecal material was fixed in filtered 4% formaldehyde and examined under a light microscope both to identify principal food sources and determine whether constituent food particles had been degraded efficiently.

Mussels were frozen at -18^{o}C, and later thawed, drained and their shell lengths, total drained weight, wet meat weight and dry meat weight (100^{o}C for 48h) were determined for each group of 7 mussels. A dry weight condition index that reflected the amount of tissue available for harvest ([dry meat weight*100]/total drained weight) was then calculated for each group of mussels.

Transplantation Experiment

Mussels of 80 mm length were transplanted from a point equidistant from each end of the third longline offshore in the central farm in Crail Bay (Fig 2). Transplanted mussels were then secured at 4m depth below an anchor marker buoy located 90m from the nearest point within the mussel farm. Previous studies had indicated that this area was exposed to a more abundant food resource than occurred at the original (source) site within the farm. The reason for the increased availability of food at this site was that no mussels were present on adjacent culture ropes. Mussels at both locations had been disturbed during the transplantation process.

Two samples of mussels were collected at 4m depth each month (24/8, 24/9, 24/10, 29/11 and 24/12/85) from sites of origin (in the farm) and transplantation (outside the farm), respectively. Each sample was comprised of 32 mussels, and was treated in an identical manner to that described above to determine shell length, dry meat weight and condition index. ANOVA was used to determine a 95% confidence interval for each sample. The growth and condition of mussels at the source and transplant locations were contrasted by dividing meat yield and condition, respectively, of transplanted mussels with that of mussels suspended from the central longline.

RESULTS

Differences in Feeding and Growth of Mussels Between Embayments

Physico-Chemical Environment

Hydrological conditions in this part of the Marlborough Sounds have been described by Flaws (1975), Tortell (1976), Heath (1982), Kaspar et al. (1985), Mackenzie et al. (1985) and Bradford and Chang (1987). Further descriptions of temporal variation of hydrological conditions in Marlborough during 1983-85 are given by Hickman, Waite, Illingworth and Meredyth-Young (in prep) and Gibbs, Hickman and Illingworth (in prep). This study attempts to define the conditions under which mussels fed and grew.

Temperature varied between 11.0 and 18.7^{o}C during 1983-4 (Fig 3a), but differed by less than 1.4^{o}C between embayments during any month. Temperature varied more at inland sites than at seaward sites, suggesting that influx of seawater at seaward sites had limited thermal variation. Plots of temperature against time had a similar form at most sites, but in Crail Bay water warmed up more slowly during spring, and reached a higher maximum temperature in summer. The maintenance of temperature differences between waters in Crail Bay and Pelorus Sound suggested that rapid exchanges of surface water did not occur between these two systems.

Salinity ranged from 20 to 34ppt during this study, and seldom fell below 30ppt in any embayment (Fig 3b). Lower salinities occurred only during a storm event in December, and after heavy rainfall in both Four Fathom and Crail Bays. Site-to-site variation in salinity was more marked in winter and spring (<8 ppt) than in summer or autumn (<2 ppt), and it is probable that low surface salinity was maintained by rainfall and freshwater runoff (M. Gibbs, DMFS, Pers Comm). Salinity was often highest and most stable in Richmond Bay where the influx of seawater maintained high salinities even after periods of heavy rainfall.

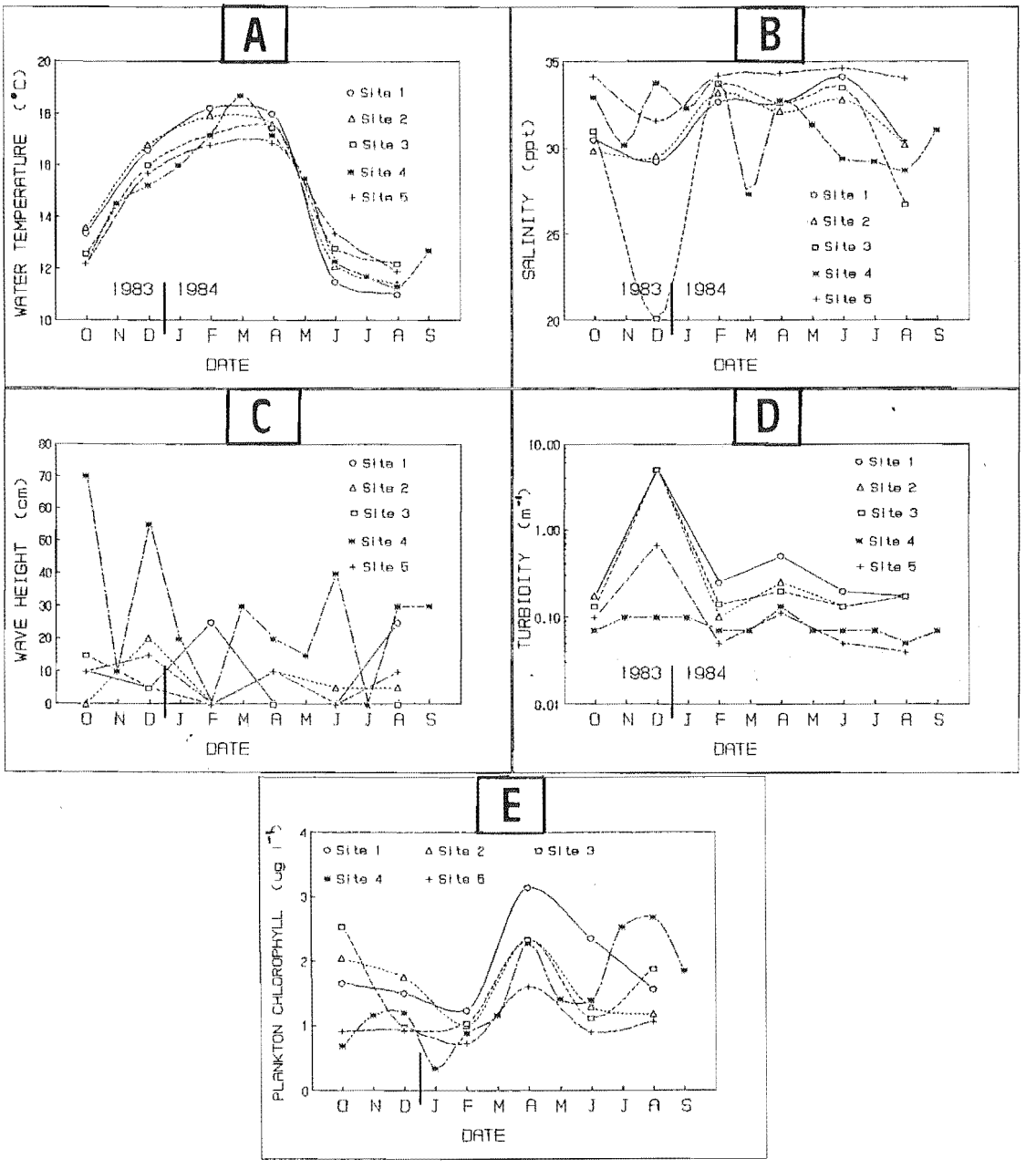

Figure 3. Environmental variation between embayments and over time (A:temperature; B:salinity; C:wave height; D:$^{-1}$/transparency; E:chlorophyll a concentration). Typical 95% CI for temperature ($0.20^{o}C$), salinity (0.79ppt), wave height ($\pm 3cm$) and turbidity ($0.13m^{-1}$) were smaller than plotted symbols. The mean 95% CI for all chlorophyll data was ± 0.26 ug l^{-1}.

Mean wave heights of 6-9cm were recorded in most embayments (Fig 3c), but in Crail Bay mean wave heights of 25-31cm were recorded and wave height sometimes exceeded 70cm. Large waves seldom developed in other embayments where high terrain provided shelter from prevalent winds.

Secchi disc transparency provided an index of suspended particulate load (Fig 3d), and indicated that water was generally less turbid towards the open sea. However, in Crail Bay turbidity was often low and similar to that in Richmond Bay. Low salinities recorded in Crail Bay suggested that low turbidity was not simply maintained by influx of seawater, and the moderate correlation ($r=-0.46$) of salinity with turbidity indicated that silt contained in freshwater runoff can explain some of the observed variation in turbidity. Similarly, silt inputs contained within floodwaters during December also resulted in the presence of turbid water at all sites except the most seaward sites of Crail Bay and Richmond Bay.

Food Availability

In different embayments, chlorophyll *a* concentrations of 0.4-3.6 ug l^{-1} were determined. The highest and lowest chlorophyll concentrations were recorded in Crail Bay, where 10 fold changes in chlorophyll occurred (Fig 3e). At most sites, less chlorophyll was present from December to March than during the rest of the year. However, phytoplankton blooms may have occurred in spring and autumn in some bays and the marked month-to-month variation in chlorophyll concentration which occurred in Crail Bay suggested that the two month interval between samples in other bays was too long to allow seasonal events in chlorophyll concentration to be demonstrated. Therefore, although this study did demonstrate changes in feeding conditions, it did not adequately describe the seasonal dynamics of the phytoplankton in different embayments.

Data for POM and PIM are not available between November 1983 and February 1984. Outside of that period, POM concentration varied from 0.7 to 3.5 mg l^{-1} between embayments, and mean POM concentrations of 2.4, 2.3, 2.5, 1.7 and 1.9 mg l^{-1} occurred at Mills Bay, Schnapper Point, Four Fathom Bay, Crail Bay and Richmond Bay, respectively. Mean chlorophyll concentrations of 1.9, 1.6, 1.5, 1.4 and 1.0 ug l^{-1} were recorded at these sites, respectively. Thus, concentrations of POM and chlorophyll declined by 30% and 46%, respectively, towards the open sea. While these changes were marked, however, separate two way ANOVA indicated month-to-month changes in POM and chlorophyll *a* (POM: $F=3.32$, $df=3$, $p=0.05$, chlorophyll: $F=4.37$, $df=5$, $p<0.01$) caused significantly more variation than temporally consistent differences between sites (POM: $F=0.92$, $df=4$, $p=0.48$, chlorophyll: $F=2.51$, $df=4$, $p=0.07$). On average one microgram of chlorophyll *a* was associated with 1.1-1.3 mg of POM, suggesting that POM concentration

ranged from an estimated minimum of 0.8 mg l^{-1} to a measured maximum of 3.5 mg l^{-1}. PIM varied from 1.3 to 9.1 mg l^{-1} between bays, except in floodwater when up to 26 mg l^{-1} was recorded. TPM usually ranged from 2.1-12.6 mg l^{-1}, but no consistent differences were found between five different embayments studied, where mean TPM varied from 6.9-8.1 mg l^{-1}. However, whereas organic matter comprised 36% of TPM in Mills Bay, it comprised only 26% of the TPM in Richmond Bay. Thus, while mean quantities and proportions of POM in particulate food resources may decline towards the sea, these differences in the quantity and quality of foods present at different sites were not established as being statistically significant over the period of my studies.

Faecal Chloropigment Content

Marked differences in the mean Faecal Chloropigment Content (FCC) of each mussel sampled occurred between the two size classes (cohorts) of mussels present within each farm during one year (15.9 vs 38.7 ug chlorophyll equivalent, ANCOVA, Table 1, $p<0.001$). After correction was made for minor differences in shell length of mussels sampled within each length class, FCC showed significant differences only between months (Table 1, $p<0.001$) and between the two different size classes (cohorts) that were sampled in each embayment ($p<0.001$). Consistent patterns of variation between the five embayments sampled were not detected during the year 1983-1984 (Table 1).

Analysis of data collected at all 14 sites sampled during the present study indicated, however, that differences in mussel size did cause variation in FCC (Section 2.2). I am not therefore confident that the differences in length of up to 20mm occurring between sites within a cohort did not affect feeding. A size corrected index of FCC was derived by dividing FCC by dry body weight. The index is used to compare

Table 1. ANCOVA table showing variation in faecal chloropigment content (FCC) of individual mussels with site, month and size class. Changes in FCC due to more minor differences in length within the two size classes sampled were corrected by using shell length as a co-variate.

SOURCE	DF	SS	MS	F	P
SITE (A)	4	752	188	0.82	0.518
MONTH (B)	5	11018	2203	9.63	<0.001
SIZE CLASS (C)	1	9202	9202	40.20	<0.001
A*B*C	43	9842	228		

COVARIATE: SHELL LENGTH (F=0.92, df=1,43) p = 0.342

the feeding of mussels both between sites and between months. This index of FCC was expected to be affected by seasonal changes in the condition of mussels, but ANCOVA indicated that the index was not significantly affected by condition in the mussels sampled within any particular size class ($F=0.32$, $df=1,18$, $p=0.58$). Caution should, however, be exercised when using this index to compare feeding by adult mussels of markedly different condition. This situation occurred between months, and between some sites in October 1983 and August 1984 (Fig 4). My presentation of results (below) therefore highlights marked differences in the FCC index that cannot be attributed to changes in condition index alone.

The use of the FCC index indicated that faecal pigment was low (5-9 ug g^{-1}) from October to February and high (16-37 ug g^{-1}) between April and August (Table 2). During each month the FCC index also showed more site-to-site variation in warm waters containing less chlorophyll *a* (December-April: 4 to 7-fold variation) than in cooler waters that contained more chlorophyll (October, and June-August: 1.6 to 3-fold variation; Fig 3, Table 2). Note that smaller differences in mussel condition occurred between sites from December to April than at other times, and changing condition alone cannot therefore explain the pronounced differences between sites. As the greatest site-to-site differences in food concentration occurred in cooler months, it is unlikely that changes in FCC over summer were due simply to mussels being exposed to a greater range in food concentration. Because the greatest site-to-site variation in FCC occurred during months in which less than 1 ug l^{-1} phytoplankton chlorophyll was recorded at some of the sites sampled, it seems likely that reduced food availability may cause the

DATE	COHORT	SITE 1	SITE 2	SITE 3	SITE 4	SITE 5	p
October, 1983	1	6.8	10.61	9.49	3.52	5.29	**
	2	2.4	9.52	14.41	3.04	12.96	***
December	1	8.2	14.2	3.1	9.0	23.4	***
	2	4.0	4.0	1.5	14.2	17.4	***
February	1	7.3	9.8	6.2	21.1	34.8	***
	2		4.1		15.7	19.6	***
April	1	67.6	62.3		10.7	76.2	***
	2	25.6	25.8	6.3	6.4	24.8	***
June	1	21.5	34.0		11.3	37.8	***
	2	19.3	15.4	15.1	22.8	13.1	*
August, 1984	1	69.3	58.4		21.2	51.2	***
	2	36.5	44.8	16.4	13.6	41.3	***

Differences between embayments:- *:p<0.05, **:p<0.01, ***:p<0.001.

Table 2. Variation in faecal chloropigment content of mussels (ug g^{-1} DW body mass) between different embayments in the Marlborough Sounds, and between mussels of 25-60mm length (1) and 60-100mm length (2).

ration ingested to decline below 1 ug l^{-1} chlorophyll *a*.

Patterns in FCC between embayments were not consistent over time, and this observation may explain why ANCOVA did not resolve trends occurring between sites. During some months mussels from Four Fathom Bay had lower FCC than mussels from other sites, but in most embayments low FCC seldom occurred in both size classes (cohorts) of mussels during the same month. Site-to-site differences in faecal pigment therefore may result from factors which did not show consistent spatial patterns. Such factors include concentrations of chlorophyll in food resources, POM in food resources, and the fraction of PIM present in the mixture of particles that are ingested.

Mussel Condition

Condition usually varied between juvenile (25-45mm length) and mature (70-100mm) mussels sampled in an embayment (ANOVA, $F>6.1$, $df=1$, $p<0.05$). However, the mussels matured at 45 mm length, and their condition did not vary significantly between the two length classes of mussels after maturation had occurred (ANOVA, $F=0.41$, $df=1$, $p=0.52$). Maturation rather than either length or cohort therefore may be an important factor determining condition.

Condition of adult mussels varied between locations (ANCOVA, $F=3.03$, $df=4$, $p=0.03$) and over time ($F=4.84$, $df=5$, $p=0.001$, Fig 4), yet was independent of shell length (ANCOVA, $F=0.23$, $df=1,19$, $p=0.63$). Condition, averaged over all sites, was found to be maximal in December (9.5%) declining to a minimum (6.9%) during August. In contrast,

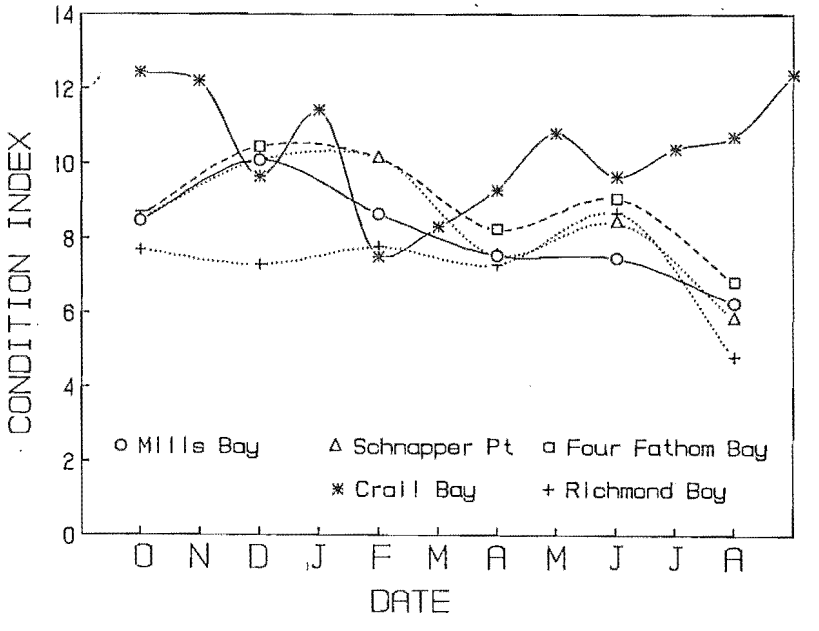

Figure 4. Changes in mussel condition between embayments and over time. Typical 95% confidence intervals for condition index (±0.37) were similar in size to the plotted symbols.

faecal pigment was lowest from October to February, and a simple relationship was not apparent between faecal pigment and condition index.

Average condition of mussels was highest (10.1%) in Crail Bay, and lowest in Richmond Bay (7.3%). However, mussels in both Crail Bay and Richmond Bay had similar mean lengths (90 vs 92mm) and faecal pigment concentrations (40 vs 55ug chlorophyll equivalent), and therefore these factors could not explain observed differences in condition.

Both hierarchical cluster analysis (using Euclidean distances) and Tukey's Test indicated that mussels in Mills Bay, Schnapper Point and Four Fathom Bay formed a single homogeneous group characterised by intermediate mean condition indices of 8%. At these three sites, condition peaked at 10% during December and declined to 6% in August the following year (Fig 4).

Mussels from the two most seaward embayments did not follow this pattern however, and in Crail Bay peak condition (12%) occurred in October, November, and August of the following year. In contrast, condition of mussels from Richmond Bay was relatively uniform and low (7%) during the first 8 months of this study, and did not exceed the condition of the intermediate group (9%) during either June or August. While plankton chlorophyll was low and PIM was maximal in Richmond Bay and may account for the poor condition of mussels, food factors alone did not account for the superior condition of mussels in Crail Bay. Additional factors, such as the rate of transport of food into mussel farms, may also therefore determine the suitability of specific sites for the purpose of mariculture.

Differences in Feeding and Growth of Mussels between Farms

Physico-Chemical Environment

Marked changes in most physico-chemical variables did not occur between different mussel farms in Crail Bay. Maximum thermal variation between farms was $0.2^{o}C$, and turbidity showed little change. As all three farms were exposed to long fetches extending in similar directions, wave height seldom varied by more than 10cm between farms. Oxygen concentration was always between 5 and 6 ppm, and showed no significant differences between farms (Kruskal-Wallis test, $p>0.05$).

Salinity was the only factor which showed significant variation between mussel farms. Moderate and inconsistent changes of up to 3ppt salinity were recorded between farms, and even within a 6h period. Low salinity coupled with slow water movement was reported in Crail Bay by Tortell (1975), and the spatial and temporal instability of salinity in Crail Bay suggested that freshwater runoff had mixed incompletely with seawater within the bay.

Water Movement

Water movement within embayments varied between ebb and flood tides. On an ebb tide 1m and 5m deep drogues moved slowly across the mouth of Portage Bay (Fig 5) and reached its southern promontory 2 hours after release. At this point, surface dye had been diluted twofold. The 5m deep drogue then moved into Portage Bay, where dye released at 5m later surfaced. The 1m drogue moved west and reached the mouth of Take In Bay 3.5 hours after release. At this point, dye had been diluted only 5 times in moving 1.7km, and the low dilution rate indicated that laminar flow had occurred over

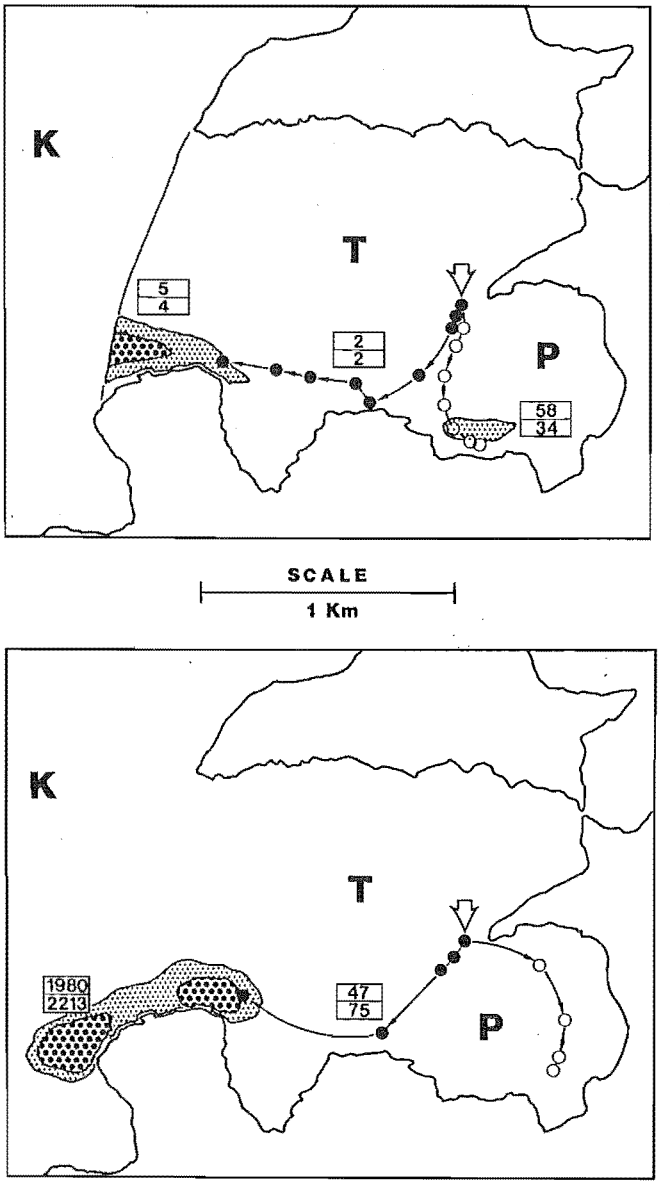

Figure 5. Movement and dilution of dye tracer in Portage Bay during ebb (above) and flood tides (below). Arrows show point of discharge of dye. Positions of 1m (closed circles) and 5m drogues (open circles) are marked every 30 minutes. Two dye dilution factors are given in boxes (see text).

most of this distance. Both the dye mass and the 1m drogue then became stationary behind a tide line separating Take In Bay from Kenepuru Sound. Dye did not move into Kenepuru Sound until slack water.

During the flood tide, the 1m drogue and surface dye moved rapidly south across Portage Bay, but the 5m drogue moved into Portage Bay. Surface dye was diluted with seawater 47-75 times during the 1.5 hours it took to reach the southern promontory of Portage Bay. Dye reached the mouth of Take In Bay only 2 hours after release, and at this point had become diluted 2000 times by seawater. This high dilution rate and the faster movement of drogues indicated that stronger, more turbulent flows occurred during flood tide than during ebb tide.

Tidal alternation of current direction did not occur in Portage Bay or Crail Bay. Portage and Take In Bays are located on an S-shaped bend in the channel of the Kenepuru Sound (Fig 1), and momentum of water flowing round this bend may carry water past the bay on the ebb tide but force water into the bay during the flood tide. This may have prevented alternation in current direction. In Crail Bay wind also appeared to inhibit bidirectional flow (see below).

As cyclic alternation of current direction did not occur in either embayment, flow of water in and around mussel farms should be determined by measurement, and not assessed by inference.

Food Concentration

In Crail Bay less variation in concentrations of chlorophyll *a*, POM and PIM occurred between farms than had occurred between embayments. Average annual POM concentration between farms ranged from 1.7 to 2.0 mg l^{-1}, and between sites mean chlorophyll *a* concentrations ranged from 1.2 to 1.6 ug l^{-1}. No significant trends were apparent between farms, but mean food concentrations were higher in the less saline waters present at the southern end of Crail Bay.

Continuous profiles showed that chlorophyll *a* concentrations 10-100m downcurrent from a mussel farm were often reduced 5-20% compared with those upcurrent from a farm (ANOVA, $F=8.72$, $df=1$, $p=0.03$) but, as water flowed beyond this distance from the farm plankton chlorophyll increased. Thus, concentrations were similar at upcurrent edges of adjacent farms, which were spaced approximately 400m apart in Crail Bay (Fig 6). At this spacing interval the presence of upcurrent farms did not appear to limit the food available within downcurrent farms.

In other areas water containing low concentrations of chlorophyll was seen to enter downcurrent farms in only 2 of 217 profiles made within sequences of mussel farms. Both farms were sited in shallow and closed embayments where slow water movement may retard mixing of grazed water originating from the farm with water

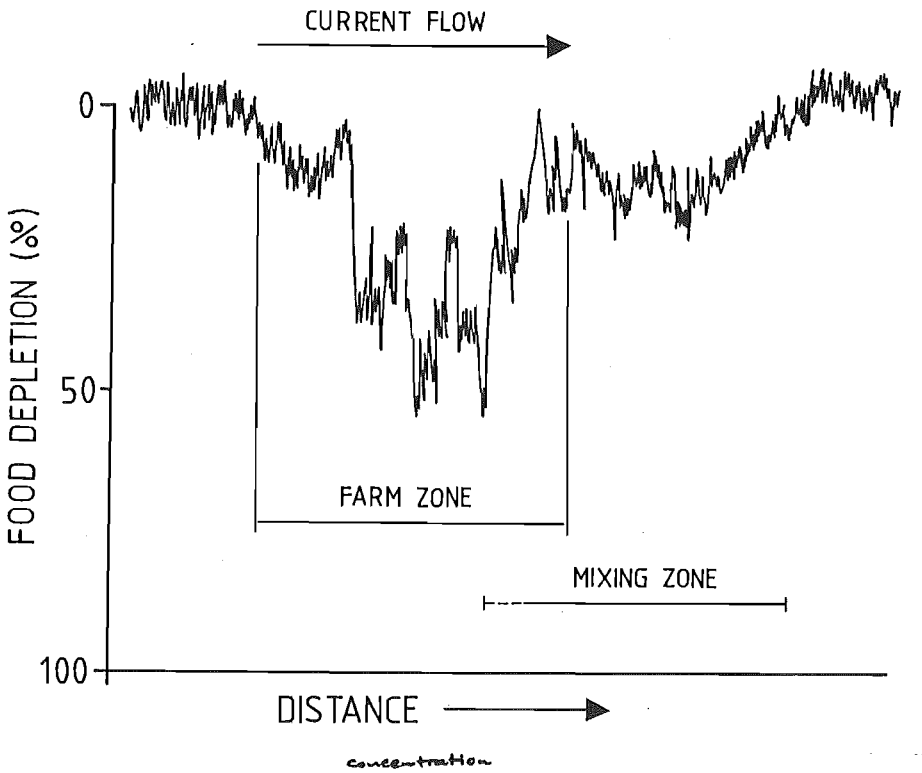

Figure 6. A profile of chlorophyll a through the mussel farm. Food concentration was depleted within the farm and recovered within the mixing zone.

which had flowed beneath the farm. Nonetheless, differences in food supply seldom occurred between farms which were situated in either Crail Bay or other embayments, and direct nutritional interference may rarely occur between farms.

Faecal Chloropigment

Even though adult mussels differing in length by 24 mm were sampled at different farms, length alone did not explain changes in in Faecal Chloropigment Content (FCC) between the three farms situated in Crail Bay (ANCOVA, see Table 3, $p=0.23$). Also, FCC did not vary consistently between farms over the twelve months sampled (ANCOVA, $p=0.60$, Table 3). Marked, spatially consistent changes in FCC did, however, occur between months ($p<0.001$).

Analysis of all data collected during my study indicated that FCC varied with mussel length (Section 2.2). FCC was again therefore divided by body mass, and the resultant index of feeding (Table 4) was used to compare results from different farms. As before, ANCOVA indicated that this index of feeding did not decline in mussels of high condition ($F=0.92$, $df=1,21$, $p=0.34$), and although a mean of 37.9 ug g^{-1}DW pigment occurred in the faeces of mussels from Crail Bay during 1983-4, lower concentrations were observed in September, October, November and January. Minimum FCC of only 11.8 ug g^{-1}DW was found in faeces of large mussels (99mm length) during January,

. Table 3. ANCOVA table showing variation in faecal chloropigment content (FCC) of individual mussels between farms and between months. Changes in FCC due to minor differences in the size of mussels sampled were corrected for by using shell length as a co-variate.

SOURCE	DF	SS	MS	F	P
SITE (A)	2	92	46	0.53	0.596
MONTH (B)	11	8145	740	8.52	<0.001
A*B	21	1825	86		

COVARIATE: SHELL LENGTH (F=1.48, df=1,21) p = 0.236

Table 4. Variation in faecal pigment content of mussels (ug g^{-1}DW body mass) between upcurrent sites on three different mussel farms in Crail Bay. Errors are given as 95% confidence intervals (ANOVA).

Date	Northern Farm	Central Farm	Southern Farm	Trend
August, 1983	19.1	19.0	18.2	
October	4.0 ±0.4	3.0 ±1.1	4.6 ±1.2	
November	4.0 ±2.4	5.2 ±2.0	(13.6 ±1.6)	
December	15.2 ±2.0	14.3 ±1.6	17.5 ±4.8	
January	1.9 ±0.1	2.9 ±0.5	2.1 ±0.2	<>
February	19.2 ±3.4	14.1 ±2.3	17.6 ±7.5	
March	21.8 ±0.4	13.1 ±1.4	10.5 ±3.8	>-
April	15.1 ±1.4	6.4 ±1.5	7.6 ±2.6	>-
May	12.4 ±1.6	11.4 ±0.4	10.4 ±1.6	
June	13.4 ±0.9	22.9 ±1.5	12.4 ±0.9	<>
July	(25.3 ±11.3)	15.8 ±2.2	18.1 ±1.2	
August	10.7 ±0.6	13.6 ±2.1	14.7 ±3.0	<-
September, 1984	(2.1 ±0.4)	9.2 ±1.3	7.5 ±1.2	

Note: The Trends column shows significant differences between farms (ANOVA: p<0.05). Bracketed data may be invalid (see text)

when chlorophyll minima also occurred in Crail Bay. Conversely, above average FCC values were found between April and August when temperature declined to its lowest value, salinity was often low, and plankton chlorophyll concentration typically exceeded 1.5 ug l^{-1}. Food availability may therefore determine FCC.

The resulting index suggested that feeding varied significantly between pairs of farms during only 5 of 13 months (Table 4, $p<0.05$). During three more months changes were induced by experimental perturbations (eg marked variation in mussel length or harvesting operations). Variation in this index in different farms only exceeded $\pm 20\%$ in only 3 of these 5 months, and rarely declined in mussels living downcurrent from other farms. Spatial changes occurring between farms in Crail Bay were of both lower magnitude and significance than those occurring between embayments (see Table 2). Most importantly, data in Table 4 provides little support for the hypothesis that the presence of mussel farms in upcurrent locations can reduce food intake by mussels living in the downcurrent farms within this sequence of 11 farms. Individual farmers may not therefore be strongly influenced by the density of stock carried on adjacent farms.

Mussel Development

Because the condition of mussels increased with shell length (ANCOVA, $F=6.84$, $df=1,21$, $p<0.01$) variation between locations and over time was determined after correction for differences in mussel size. After correction, condition showed no marked difference between the three similar farms sampled (ANCOVA, $F=0.21$, $df=2$, $p=0.81$), a result strongly supported by viewing data presented in Figure 7a. However, condition showed marked change between months (ANCOVA, $F=10.7$, $df=11$, $p<0.0001$). Over time, mean condition of the adult mussels sampled declined from 12.1% in October to 7.6% in February, then rose again to 11.9% in September.

The average condition of adult mussels in Crail Bay was 10.1%, and condition fell below 10% during only December, February, March and April when low faecal pigment concentrations are recorded. In January, however, minimal faecal pigment was recorded but condition increased to 11.0%. This apparent discrepancy between condition and nutrition may have been the result of (1) recovery from spawning which occurred prior to December, and/or (2) an unrecorded improvement in feeding conditions over the preceding month (possibly initiated by mineral inputs during a flood event that occurred during December).

Condition exceeded 10% in November, and from May to September. Prior to and during this period of high condition, temperatures were low, salinities declined, and concentrations of chlorophyll and POM were high.

Variation in mussel length between farms may have obscured changes in meat yield between October and April. However, after transplantation of mussels from the central farm to northern and southern farms in May, mussels of similar size were sampled on all farms. Dry meat weight then increased more rapidly on an unstocked longline in the northern farm than on fully stocked longlines in other farms (Fig 7b).

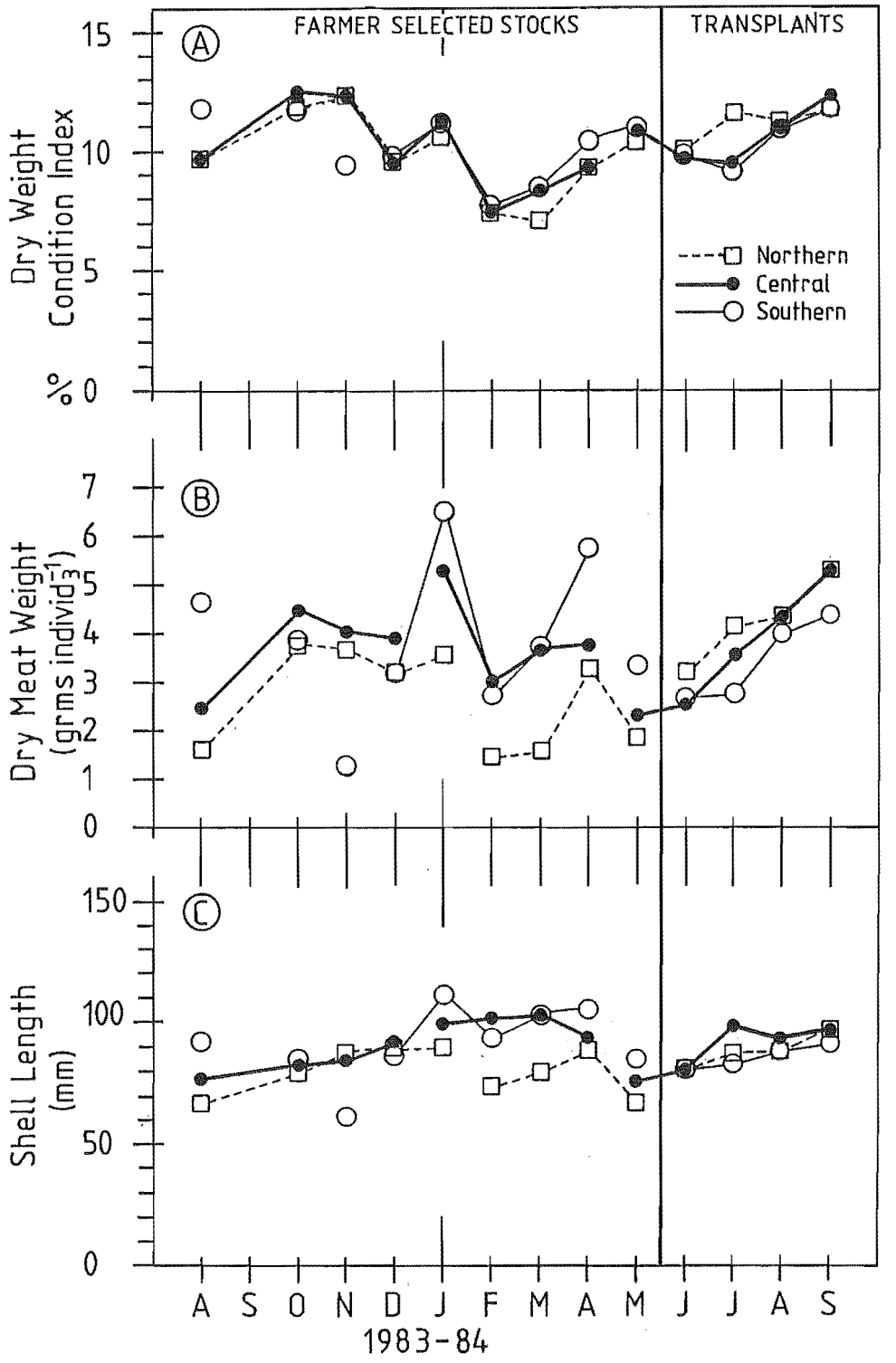

Figure 7. Variation in condition index (A), tissue weight (B) and length (C) of mussels in different farms in Crail Bay, and over time. Typical 95% confidence intervals for condition index (±0.4%), tissue weight (±0.2g) and shell length (±1.8mm) were smaller than the plotted symbols.

After this unstocked longline was restocked, similar, high meat yields occurred in northern and central farms, but lower meat yield was recorded for mussels grown on a heavily stocked longline in the southern farm. Thus, high meat yield may occur on longlines that carry less stock.

Differences in Feeding and Growth of Mussels within the Farm

Physico-Chemical Environment

Little physico-chemical heterogeneity was recorded in a mussel farm. Although oxygen tension, salinity, turbidity, temperature and wave height were recorded along the length of a longline, only wave height showed modest but significant attenuation within the farm. During any month, no significant change was recorded in other physico-chemical parameters.

Nixon et al. (1971) recorded a substantial reduction of oxygen concentration in water flowing over a colony of *M. edulis*, but oxygen uptake by *P. canaliculus* did not result in significant depletion of dissolved oxygen in the central farm in Crail Bay.

Water Movement

Flow velocity did not change markedly with depth outside farm boundaries in Crail Bay, but marked attenuation of flow occurred both between two pairs of longlines, and between two longlines comprising a pair (Fig 8).

In the 20m wide channels between pairs of longlines, water flowed at 0.07 m s^{-1} from 0-6m depth, whereas three times this velocity flowed beneath the farm, and flow varied substantially with depth (Kruskal-Wallis Test, p=0.001).

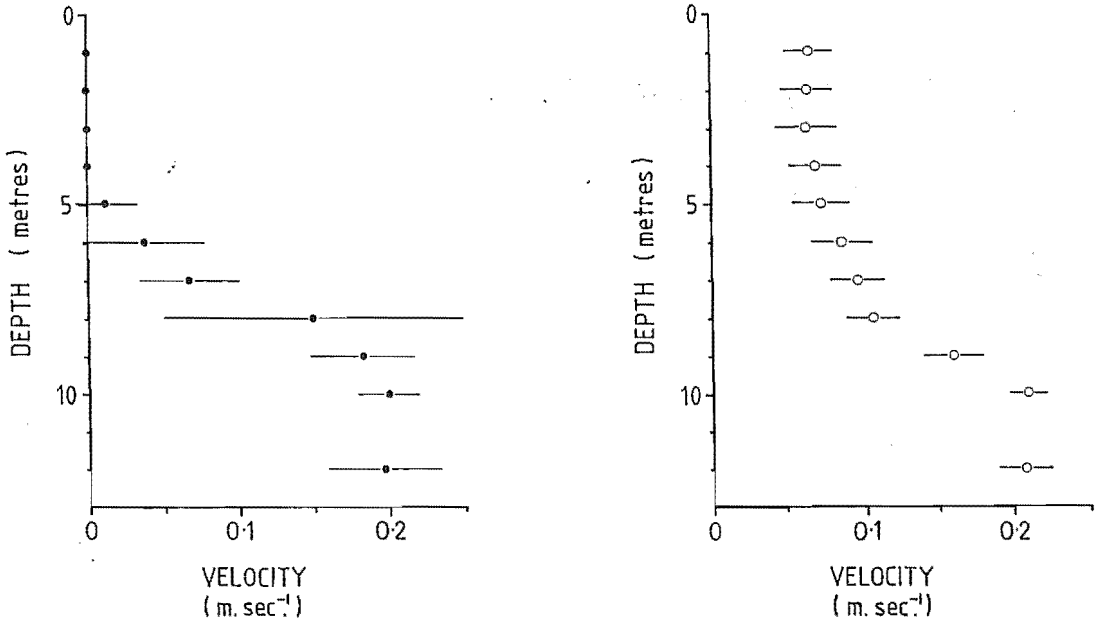

Figure 8. Variation in flow velocity with depth (left: between two longlines, right: in channels between pairs of longlines [see text]).

Observations made between two longlines spaced 0.8m apart by a buoy, indicated that no flow was detectable 0-4m below this buoy, yet water flowed at 0.01 m s^{-1} at 5m depth. Flow then increased further to 0.03 m s^{-1} at 6m, the maximum depth occupied by mussels. Below this depth flow increased more rapidly to a maximum of 0.20 m s^{-1} at 12m depth. Marked variance in flow at a depth of 8m indicated that unstable boundary layers may exist between water moving slowly past culture ropes and water flowing at higher velocities beneath the farm. Again, therefore, the data indicated that current speed varied markedly with depth (Kruskal-Wallis Test, $p=0.001$).

By comparison, continuous records showed that flow inhibition was persistent throughout a two month survey. Flows were 44% slower one metre from the centre of a longline supporting 55mm long mussels (3m depth:0.035 $\pm$0.004 m s^{-1}) than below (10m depth: 0.058 $\pm$0.004 m s^{-1}) and offshore from (3m depth: 0.066 $\pm$0.005 m s^{-1}) this central farm in Crail Bay (Standard Errors Test, $p<0.01$). In contrast, flows were 66% slower adjacent to the larger 100mm long mussels present during the first study (Fig 8).

Marked variation occurred between flows recorded below and offshore from this central farm (Fig 9a,b). Anomalies in current speed and direction between these sites suggested that substantial variation in flow occurred either over a horizontal distance of 200m or a vertical distance of 7m. At most times, marked vertical stratification of currents did not occur between 1 and 10m depth outside the farm, and it seems more likely that flow varied with horizontal distance.

Wind also affected flow through Crail Bay. During the two months when current meters were deployed, southerly flow did not occur in winds which had a strong NE vector (Figs 9a, 10), and simple bidirectional flow occurred only during SW winds (Fig 9b). Outside the farm, NE winds induced monodirectional flow less consistently than within the farm. However, protracted periods of monodirectional flow still occurred in strong NE winds. Thus, winds blowing parallel to both the shoreline and the longline modified food transport in the bay and through the farm.

The direction of flow through the mussel farm was strongly aligned with the angle of the longlines, in contrast to flows recorded beneath the farm (Fig 9). Longlines were not highly permeable to transverse currents and may have acted as barriers which deflected the path of incident currents. This was tested using regression analysis (below).

Currents were divided into vectors parallel to and transverse to longlines. The use of these vectors in regression analysis doubled the proportion of variance explained (adjusted $R^2=0.44$, $p<0.0001$) compared with untransformed current speed. Considering that variance was also caused by limited directional sensitivity of current meters at slow current speeds this fit was quite good. In the fitted model, flow through the mussel farm studied was promoted by vectors flowing parallel to the longline (T-statistic=-8.88,

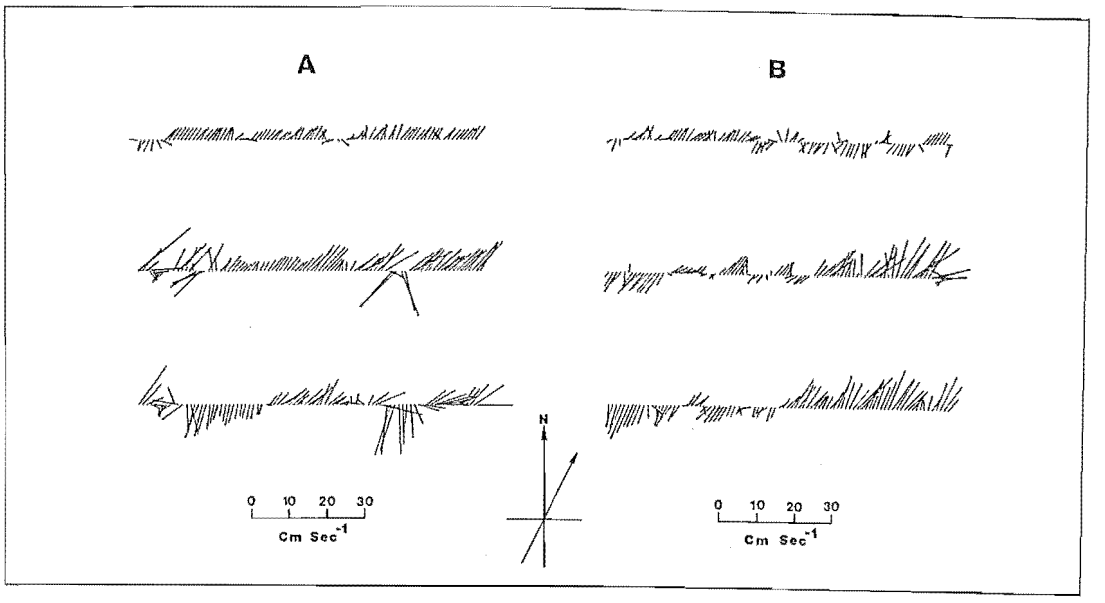

Figure 9. Stick Plots of flow in (top), beneath (middle), and offshore from a mussel farm (below) during NE (A), and SW (B) winds. Sticks show hourly flow vectors; lines of stick give four days records at each site. The oblique arrow on the compass rose shows longline alignment.

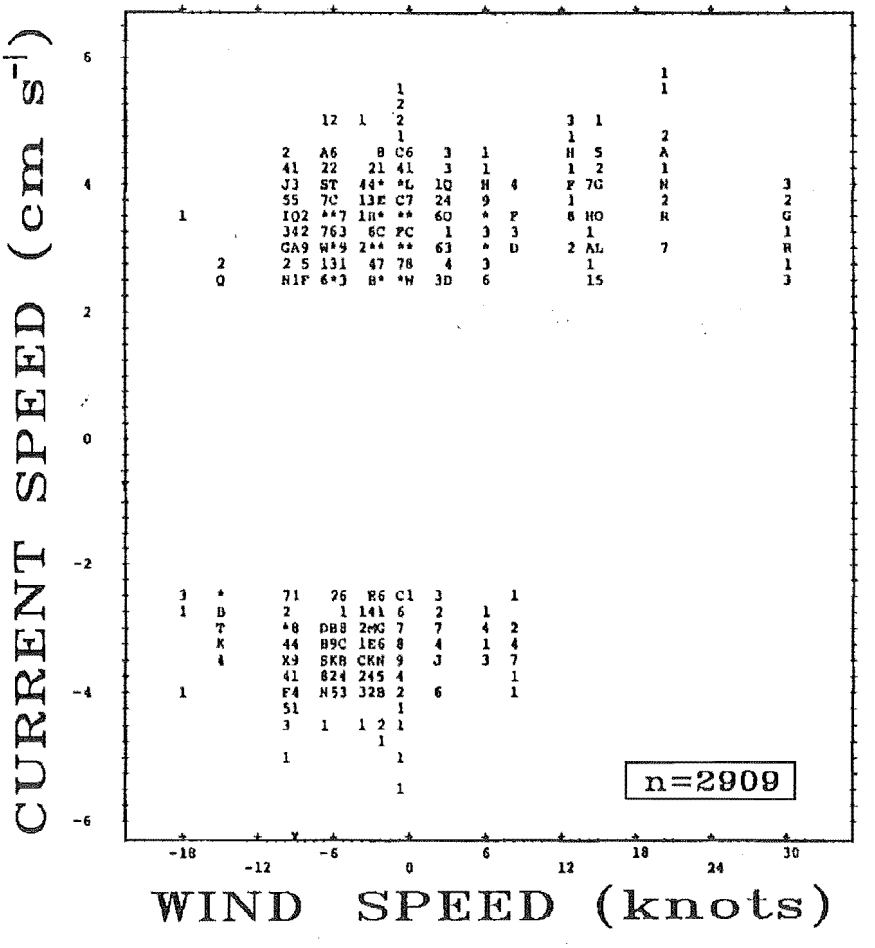

*Figure 10. Effects of wind vectors parallel to longline systems on the direction and velocity of water movement through the farm. Numeric values represent the number of observations at any point, alphabetic characters represent 10 (A) to 35 (Z) observations, * represents more than 35 observations.*

$p<0.001$) yet transverse currents did not promote flow. As oblique currents promoted little flow, the angle at which currents struck longlines was a major determinant of the rate of transport of food through the mussel farm.

Food Concentration

Mean chlorophyll *a* concentration was reduced up to 60% as water flowed through the farm (ANOVA, $F=4562$, $df=1$, $p<0.0001$). Therefore, food concentrations declined up to 10 times more strongly within the area occupied by the mussel farm than concentrations had declined between adjacent farms. Thus, the presence of mussel stock was associated with highly significant reductions in plankton chlorophyll.

Whereas chlorophyll *a* profiles showed that phytoplankton concentration was stable upcurrent from a mussel farm, chlorophyll declined markedly within the farm (Fig 6, ANOVA, $F=1966$, $df=1$, $p<0.0001$). Within the central area of the farm studied, chlorophyll had fallen, on average, by 44% (Fig 6), and minimal values occurred before the downcurrent ends of longlines were reached. Thus, whilst chlorophyll concentrations subsequently increased as water flowed past the downcurrent end of the farm, substantial reductions of food concentration occurred within mussel farms.

The proportion of phytoplankton removed as water flowed through a farm varied in space and time, and different chlorophyll concentrations also often occurred along 10m sections of longline (Fig 6). Differences in chlorophyll concentration within the farm suggested that local changes in flow or feeding occurred, and affected the amount of food depletion induced by mussel feeding. Mussels consumed 13% and 52% of chlorophyll in two similarly stocked farms, and food depletion increased from 5% to 19% over one tidal cycle. These changes may be caused by variations in current speed which regulate the length of the period during which water can be cleared of food by mussels. Seasonal changes in the level of food depletion were also evident as maximum amounts of food depletion found within the farm during any month decreased markedly between May (19%) and July (1%), and over this period water temperatures decreased from 16 to 11^{o}C and food (chlorophyll *a*) concentrations increased two-fold in Crail Bay. It is likely that either low temperature or high food concentration caused decreased filtration and reduced rates of food removal by mussels.

Faecal Phytopigment

Although variations in Faecal Chloropigment Content (FCC) was generally unrelated to variation in mussel length between sites in the central farm in Crail Bay (ANCOVA, $F=1.63$, $df=1,21$, $p=0.22$), the length of mussels sampled during one month varied by less than 7mm. Marked reductions in FCC, however, occurred in months characterised by high temperature and low chlorophyll, and others typified by low

temperature and high chlorophyll (Table 5, $p<0.0001$; Table 6). Interestingly, therefore, plankton chlorophyll was indicated as a covariate of faecal pigment ($p=0.05$), and may determine feeding within mussel farms.

After dividing FCC by body mass to allow comparison between locations distributed at different levels of organisation (see methods), this index of feeding was again found to be independent of mussel condition (ANCOVA, $F=3.00$, $df=1,21$, $p=0.10$).

Table 5. ANCOVA table showing variation in faecal chloropigment content (FCC) of individual mussels between sites within one farm and between months. Changes in FCC due to differences in food concentration were corrected by using plankton chlorophyll as a covariate.

SOURCE	DF	SS	MS	F	P
SITE (A)	2	67	33	0.31	0.7339
MONTH (B)	11	10383	943	8.72	<0.0001
A*B	21	2273	108		

COVARIATE: PLANKTON CHLOROPHYLL ($F=4.22$, $df=1,21$) $p=0.05$

Table 6. Variation in faecal pigment content of mussels (ug g^{-1} DW body mass) between three different sites within a mussel farm in Crail Bay. Errors are given as 95% confidence intervals (ANOVA).

Date	Upcurrent Site	Midfarm Site	Downcurrent Site	Trend
August, 1983	19.0	14.1	10.2	>>
October	4.3 ±0.4	3.3 ±0.5	3.1 ±1.1	>-
November	15.2 ±0.5	14.4 ±1.8	10.2 ±1.9	->
December	14.3 ±1.0	13.5 ±1.9	14.4 ±1.0	
January	3.0 ±0.6	2.4 ±0.9	1.5 ±0.4	->
February	14.1 ±2.3	7.9 ±0.7	11.2 ±0.9	><
March	13.1 ±1.4	11.3 ±0.8	13.9 ±3.6	>-
April	10.7 ±1.5	13.3 ±1.0	7.5 ±1.5	<>
May	14.5 ±0.4	12.6 ±1.4	11.4 ±1.7	>-
June	22.9 ±1.5	17.6 ±2.4	11.9 ±2.1	>>
July	15.8 ±2.2	21.0 ±2.9	17.6 ±3.6	<-
August	21.6 ±2.1	15.5 ±1.2	15.9 ±2.4	>-
September, 1984	9.2 ±1.3	6.1 ±0.6	6.4 ±1.0	>-

Note: The Trends column shows significant changes between the two adjacent pairs of sites within this farm.

In 10 of 13 months, paired contrasts made during single months then indicated that faecal pigment declined markedly between similar mussels that fed in upcurrent and downcurrent areas of the farm, respectively (Table 6). This pattern of reduced feeding by mussels inside the farm boundaries was a persistent phenomena and, over the year, means of FCC declined by 23% (centre of longline) and 20% (downcurrent site) when compared with that at the upcurrent edge of the longline. Furthermore, during 3 of 13 months sampled, FCC was reduced more than 50% at downcurrent sites and these marked declines in FCC were associated with reduced plankton chlorophyll at downcurrent locations on the longline. It should be noted that most physico-chemical parameters showed no significant variation within the farm (above), and only factors determining food supply appeared to explain this reduction in feeding. Current speed and food concentration (as indicated by chlorophyll, PIM and POM) were the only factors which showed significant variation along the longline, and either factor may have induced the decline in food uptake within this farm situated in Crail Bay.

Mussel Development

Shell length of mussels increased at uniform rates throughout the year (Fig 11c), but the two size groups of mussels showed different rates of growth. Regression coefficients suggested that shell length increased at a rate of 4.7 mm month^{-1} in the first cohort (72-107mm length: sampled August to May), and 6.9 mm month^{-1} in a second cohort (43-96mm length: July to September). Differences in rates of shell growth can be attributed either to variations in environmental factors, including seasonal factors, or differences between the two cohorts studied.

Although the rate of increase in shell growth varied little within a cohort, tissue growth varied markedly over time, and also showed negative development from December to March. Whereas this was part of the period during which reduced FCC was recorded throughout Crail Bay, spawning during summer may also account for such changes.

During the year studied, the condition of adult mussels varied markedly between months (ANOVA, $F=44.7$. $df=11$, $p=0.001$). In addition, pairwise comparison indicated that condition index, meat yield and length often varied on one longline (Tukey's Test, $p<0.05$, Fig 11). Thus, mussels from the centre of a longline were 5% shorter and, on average, 5% lower in condition, had 8% less drained weight and yielded 16% less dry meat than those from the end of each longline.

Alternation of current direction resulted from both tidal and wind action, and could prevent consistent differences in food concentration and feeding from occurring along the longline. Alternating currents could therefore obscure the impact that food depletion had on meat yield within the farm, and for this reason a transplantation trial

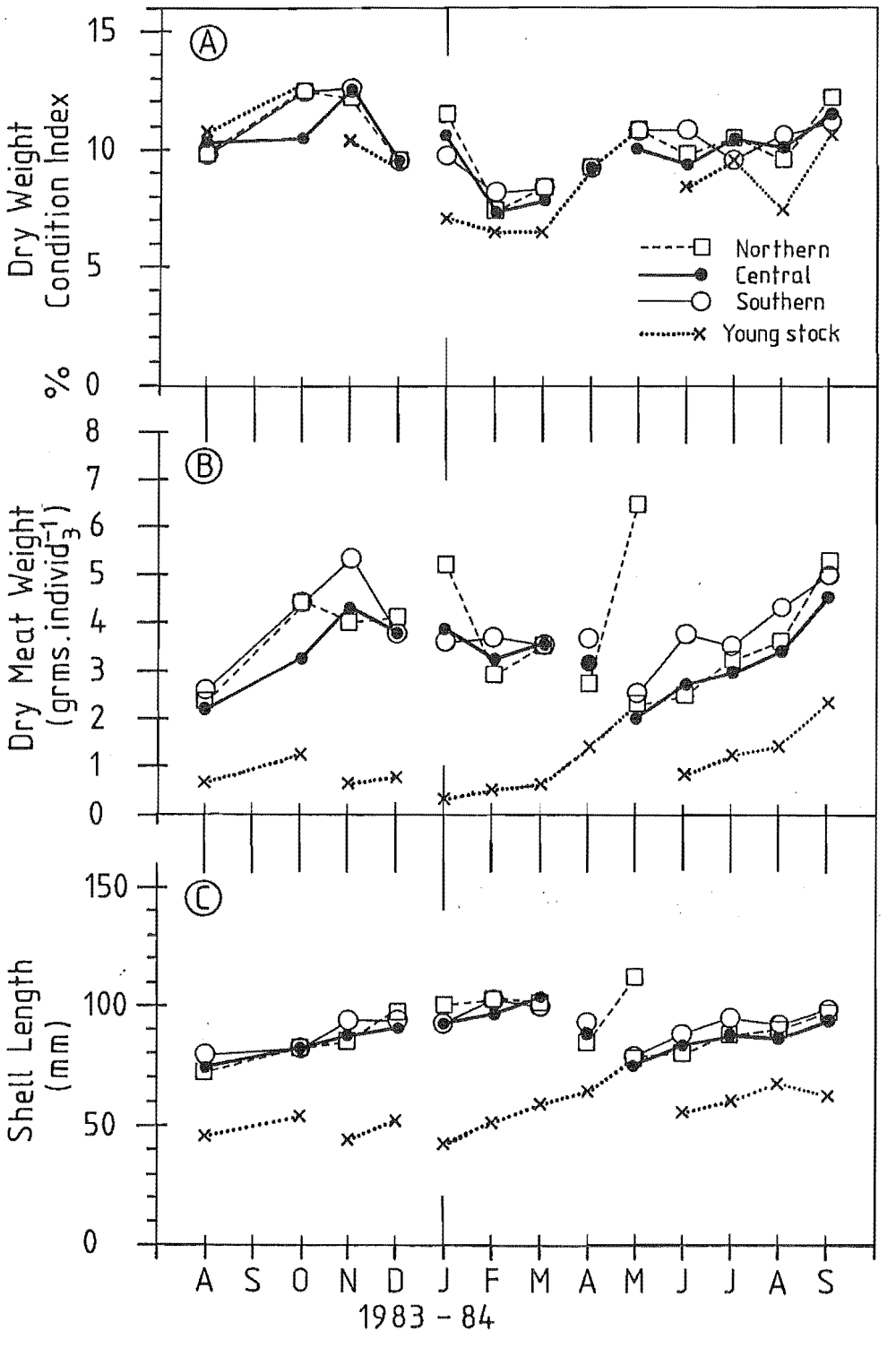

Figure 11. Changes in condition index (A), tissue weight (B) and length (C) of mussels between positions on a longline, and over time. Typical 95% confidence intervals for condition index (±0.4%), tissue weight (±0.2g) and shell length (±1.8mm) were smaller than the plotted symbols.

was conducted (below).

Growth of Transplanted Mussels

When mussels were transplanted from the centre of a longline to an area outside the zone depleted of food they showed a 19% increase in meat weight and a 16% increase in condition index after one month (ANOVA, $F>26.6$, $df=1$, $p<0.014$, Fig 12) compared with a control group of mussels suspended from the longline at the source site (see methods). Temperature increased from 13 to 16°C during the next three months, and substantial but less marked enhancement of meat yield and condition was recorded in mussels feeding outside the farm. Four months after transplantation, a marked reduction in condition indicated that the mussels outside the farm had spawned. During most of this short transplantation experiment, however, improved meat yield occurred after moving mussels from an area of the farm which was depleted of food, to an area which contained more food.

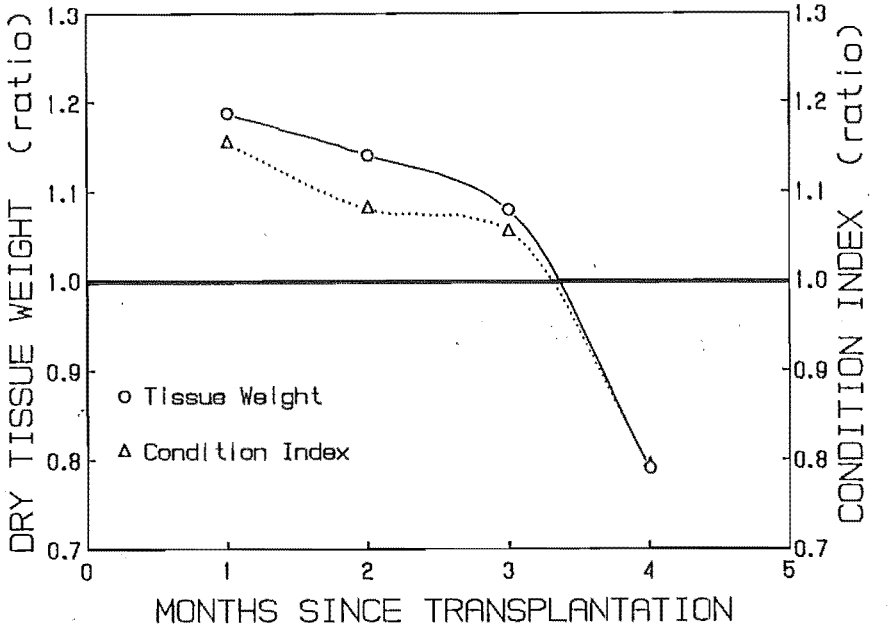

Figure 12. Increases in tissue weight and condition of mussels which had been transplanted outside the zone of food depletion, compared with mussels living in the farm (all differences were significant at $p<0.05$).

DISCUSSION

Traditional eco-physiological perspectives emphasize the importance of responses of individuals to an external environment (Smith 1986) which changes in space (Beklemishev 1961; Bowman et al. 1981) and time (Iverson 1977; Schwind 1977; Thompson 1981). Analysis of how feeding and growth responses vary over these time-space scales is therefore needed if one is to understand how environmental constraints affect success of biological communities (Schoener 1971; Haury et al. 1977; Smith 1986). Such an analysis can also indicate the scales at which research and development effort should be concentrated. During the present study, major changes in environmental conditions, feeding and growth occurred both at two geographic scales, and over time. This discussion considers why feeding and growth of mussels varied between embayments, within farms and between months.

[Scale 1] Between embayments

Marked variation occurred in the rates of feeding and growth of *P. canaliculus* between embayments. This was not unexpected as the growth of other species of mussels (eg Quasim et al. 1977; Incze et al. 1980; Mallet et al. 1987) and other bivalves (Chantry et al. 1983; Essink and Bos 1985) also varied markedly between areas spaced a few kilometers apart. It is interesting, however, that mussels from Crail Bay and Richmond Bay showed consistently higher and lower condition respectively than mussels from other bays. Spatial differentiation of the Marlborough Sounds into areas promoting high, medium and low condition indicates that some embayments are more suitable for mussel mariculture than others.

Some discrepancies occur between my results and those of Hickman et al. (in prep.) who studied spatio-temporal changes in condition of *P. canaliculus* in Marlborough using a different condition index. While both studies indicated that mussels had high condition in Crail Bay, Hickman et al. (in prep) recorded maximal condition in Mills Bay where I found mussels of medium condition. Both studies record low condition in the outer Pelorus Sound, but Hickman et al. (in prep) suggest that mussels of low condition also occurred in Four Fathom Bay where I found mussels of moderate condition. Discrepancies between the studies were not marked, but may indicate that variation occurs between farms in each embayment, and such variation could obscure some variation between embayments and over time. However, Hickman et al. used cooked meat weight, rather than dry tissue weight, to determine condition and variation observed between studies may also therefore reflect this methodological difference.

Many factors may affect growth of bivalves. Growth rate may decline when

food concentration or quality is reduced (Incze et al. 1980; Stromgren and Cary 1984; Hummel 1985; Enright et al. 1986; Page and Hubbard 1987), in conditions of slow mineral flux (Carricker et al. 1980), extreme salinity (Chantry et al. 1983; Weinberg 1985; Quasim et al. 1977), high (Maung-Myint and Tyler 1982; Shumway and Newell 1984) and low (Bayne and Worral 1980) temperature, high current speed (Kirby-Smith 1972; Wildish et al. 1987), low oxygen tension (Riisgard and Poulsen 1981) or high growth density (Weinberg 1985).

The range of factors that affect condition and tissue growth in *P. canaliculus* is not known, but previous studies found that environmental parameters were uncorrelated with rates of shell growth Flaws (1985), and that either low salinity or high food concentration enhanced condition of *P. canaliculus* Hickman et al. (in prep). The apparent difference between these two studies may be explained by the negative correlation of shell growth and tissue weight observed during summer in Crail Bay. This observation supports the contention that growth of shell and tissue are not always linked phenomena in bivalves (Hilbish 1986; Borrero and Hilbish 1988). In my study, slow current speed, low food concentration, high salinity and high temperature were identified as factors which may limit feeding and growth of *P. canaliculus*. Whereas food supply, temperature and salinity can have a direct effect on feeding (see Sections 2.2 and 3), current speed did not affect feeding directly (Section 3.2) and an indirect role for current speed in limiting feeding rate is postulated below.

Dense communities of bivalves depend on a continual influx of food to support growth (Hummel 1985b; Frechette and Bourget 1985). Dense communities of *P. canaliculus* cleared substantial proportions of the food flowing past farmed populations, and local depletion of food limited both its food intake and growth. Food depletion appeared to occur when rates of food consumption approached rates of influx of food, and this balance between food supply and consumption may limit the maximum viable size of farm communities. Farm communities become isolated from their food supply during periods of slow current flow, and adequate flow of water through an embayment is essential for successful mussel cultivation.

In the absence of extant information on biological needs of *P. canaliculus*, marine farming permits have been allocated on the basis of competition with other water users. This has encouraged development of farms within embayments. Entrapment of fine sediment in such embayments (Lauder 1987) indicates that reduced flow occurs within them. Farms may therefore become isolated from food bearing currents and as a result they are likely to provide sub-optimal conditions for intensive mussel culture.

Position, bathymetry and wind action affect flow in embayments and may interact to create a unique flow pattern at a particular site. Flow is a partial determinant of carrying capacity of mussel farms (Rosenberg and Loo 1983; this study),

and so different optimal stocking strategies probably exist for farms located in different embayments. We now need to establish both the factors that limit flow through embayments, and how flow affects the carrying capacity of farms exposed to different concentrations of food.

Pursuit of this understanding should become a research priority. Few farms have been developed in open embayments and channel systems, but many farms are situated in closed embayments where slow movement of water may limit stock density. Stronger currents flow in major channel systems (Heath 1982) than I recorded in embayments, and these channel systems may represent areas which can support high stock densities and rapid growth. Thus, there may be a need to re-evaluate the criteria currently used to define those sites that are suited to the intensive culture of mussels.

[Scale 2] Between farms in an embayment

Contrary to the expectation of some mussel farmers, no nutritional interference was recorded between adjacent mussel farm communities. No decline in either food concentration, feeding or growth was recorded in a sequence of 11 adjacent farms in Crail Bay, and food concentration seldom declined between mussel farms located in other embayments. The distance of 300-400m which separated farms during my study therefore was adequate to prevent direct nutritional interference occurring between them. However, it should be noted that slow water movement or reduced separation between farms could cause such interference to occur.

My study has indicated that productivity of farmed mussels was not affected by mussels living on neighboring farms, and indicated that the viability of individual farms may be strongly dependent on selection of an appropriate site and the use of an appropriate management strategy.

[Scale 3] Within farms

The present study suggested that complex nutritional relationships exist between current speed, food availability, and feeding and growth within mussel farms. Understanding these relationships should provide the key to improving the productivity of mussel farms.

Current speed is a vital factor in dense cultures of *M. edulis* (Rosenberg and Loo 1983), and my study proved that flow inhibition occurs in the mussel farms in Marlborough. Presence of culture ropes retarded flow of water and extended the period that water was grazed by mussels. The particular importance of flow retardation is that it probably reduced the quantity of food filtered by mussels. In other studies, the

physical structure of mussel farms has not been shown to restrict flow (Cabanas et al. 1979; Rosenberg and Loo 1983; Rodhouse et al. 1985), but flow inhibition probably does occur in other culture systems. The close proximity of longlines and small spacing between culture ropes in mussel farms in New Zealand may accentuate the magnitude of flow inhibition, and thereby impose a significant constraint on productivity.

Slow diffusion of food across boundary layers limited the growth of dense bivalve communities (Wildish and Kristmanson 1979), and depletion of food also limited growth of *M. edulis* in slow moving boundary layers enclosing a benthic colony (Frechette and Bourget 1985a,b). Depletion of food also occurs around other colonies (Glynn 1973), causing food concentration to limit growth (Buss 1981). Thus, my findings are not unexpected.

Several studies have shown that marked food depletion can occur in farmed communities of *M. edulis*. Food depletion caused by feeding of *M. edulis* varied from 60% in the Rias of Spain (Cabanas et al. 1979), 15-50% in Sweden (Rosenberg and Loo 1983) and 30-60% in Ireland (Rodhouse et al. 1985) at current speeds of 2-10 cm s^{-1}. *P. canaliculus* also consumed 15-60% of available food at similar, slow current speeds.

Environmental conditions under which these determinations of food depletion were made need to be compared before causes of these high rates of food retention can be understood, but details of conditions have not been specified by all authors. All studies were apparently conducted at concentrations of 0.5-6.0 ug l^{-1} chlorophyll, 0.3-3.5 mg l^{-1} POM, and 30-36ppt salinity (Korringa 1976; Cabanas et al. 1979; Rodhouse et al. 1984, Rosenberg and Loo 1983; this study). However, temperatures of 10-12^{o}C (Cabanas et al. 1979) and 12-18^{o}C (this study) were recorded on days that food depletion was determined, and annual ranges of 8-18^{o}C (Rodhouse et al. 1984) and 0-15^{o}C (Rosenberg and Loo 1983) occurred in areas where the other studies were conducted. As *M. edulis* maintains "a high level of filtration even in temperatures down to -1^{o}C" (Loo and Rosenberg 1983), perhaps temperature did not affect food depletion markedly, and the range of food depletion recorded reflected the limited impact of environmental variation on filtration rate. Many other authors, however, found marked variation in filtration with temperature (eg Sprung 1974b; Schulte 1975; Section 3.3.2) and so thermal variation may explain seasonal changes in the magnitude of food depletion around *P. canaliculus*.

It is clear that the magnitude of food resource depletion could require management when either feeding or growth of mussels is limited by low food concentration, and both conditions occurred in downcurrent areas of the farm during the present study. A farm's structure determines both the rate of removal of food by mussels, and distribution of mussels with respect to the food resource. Thus, manipulation of the farm structure can be used to reduce both the magnitude and

impact of food depletion.

However, food concentrations at which stock should be redistributed to reduce the impact of food depletion on growth is not adequately defined by this or previous studies. Rosenberg and Loo (1983) suggest that stock density can be increased until mussels ingest a maintenance ration at the downcurrent edge of the farm, but this suggestion is inadequate as the viability of mariculture systems depends on sustaining a rapid growth rate, and not merely on maintaining growth. Substantially higher concentrations of food are needed to promote the continuous, rapid growth required of an optimised cultivation system.

Food limitation of grazing occurred throughout the year in Crail Bay, but was pronounced at food concentrations below 1 ug l^{-1} chlorophyll *a*. An absence of physico-chemical differentiation of water inside mussel farms (eg oxygen concentration, salinity, and temperature) suggested that poor feeding was not caused by abiotic factors. However, while the food concentration outside a farm was frequently sufficient to provide mussels with full rations of food, reduced food concentrations inside farms often reduced food consumption to levels below the threshold of satiation (see Section 2.2). Reduced food availability in the farmed area was probably a principal cause of reduced feeding within Marlborough farm communities. Intraspecific competition for food therefore may limit growth of farmed, as well as natural (Frechette and Bourget 1985) communities of mussels.

These negative impacts of food depletion on feeding and growth can be moderated by redistribution of stock and redesign of farm structures. However, a detailed understanding of the structure and function of farm communities is required before optimised farm structures can be developed.

In Crail Bay, longlines were relatively impermeable to currents and no flow was measured across pairs of longlines. Flows were deflected and ran parallel to longlines, even when transverse currents flowed beneath the farm. This indicated that Sullivan's (1978) model of fluids striking an impermeable plane could be used to describe flow past longlines. In both Sullivan's model and my study, current vectors parallel to longlines were translated into flow, whereas transverse vectors were absorbed by longlines. Sullivan's model therefore may be useful for modeling the balance between supply and consumption of food in farms situated in waters moving at different speeds and containing different concentrations of food. Development of a new model pertinent to New Zealand conditions is not advised until more comprehensive descriptions are available of the movement of water through, around and beneath different farm structures.

During my study, flow of water was promoted by the influx of water at the upcurrent end of a mussel farm, and the flow induced by this influx was attenuated by

absorption of energy contained in current vectors at right angles to the longline. However, flow may also be motivated by viscous drag between fast moving currents flowing beneath a farm and slow moving currents flowing through farms and attenuated during turbulent contact with longlines (Davis 1986). The following factors may regulate transport of food through the mussel farm, and should be investigated further:

1) angles between longlines and prevalent currents,
2) separation between adjacent pairs of longlines,
3) length and depth of longlines, and,
4) stock density, size and distribution.

It must be understood that critical evaluation of these factors is required before they are incorporated into models of the influx and uptake of food within mussel farm communities.

Marked benefits may be derived from this evaluation. The farm where mussels were transplanted outside of the zone depleted of food had already been modified to reduce food depletion, and this modification had resulted in a "10-15% increase in meat yield" (G. Clarke, Pers Comm). After stock was transplanted, meat yield increased 18%. Increased yield of at least 18%, and up to 33% can therefore be obtained by modifying structures in moderately stocked farms. Only 10% improvement in meat yield should increase profit from one pair of longlines by NZ$1,150-1,430 per annum (data from Sanford South Island Ltd.), and produce NZ$1.2m of exportable product (data from Weeber 1987). A minimal (10%) estimate of increased meat yield suggested that marked returns can be generated by redesigning moderately stocked farms, and up to three times these returns may result. Increased food depletion and more pronounced loss of yield is predicted in more heavily stocked farms, and in such farms substantial improvements in both yield and profit can be obtained by manipulating the distribution of stock.

SECTION 2.2.

Impacts of environment, food concentration and growth on the feeding and condition of the mussel Perna canaliculus: a multivariate analysis

ABSTRACT

Both Particulate Inorganic Matter (PIM) and plant pigment were used to measure feeding by *Perna canaliculus*. Only 26% of PIM present in food was found in faeces. This loss of PIM probably occurred due to rejection in pseudofaeces, uptake from the gut or leaching from faeces. Pigment assays were therefore used to determine feeding by farmed mussels.

Filtration was maximal and ingestion became limited by food availability below a food threshold of 1.5 ug l^{-1} chlorophyll *a*. Above 1.5 ug l^{-1} chlorophyll, filtration rate declined as food concentration increased, but maximal ingestion rate was recorded. Filtration rate and ingestion rate also increased markedly with both shell length and water temperature.

Assimilation efficiency was negatively correlated with temperature.

Condition index increased with mussel length, and declined as temperature increased. At low food levels (< 1.5 ug l^{-1} plankton chlorophyll), food concentration and clearance of food from water may limit condition. At high food levels, the ingestion of PIM may displace digestible foods from the diet and limit mussel condition.

No other factors were identified which exerted major influences on the biology of *P. canaliculus* within the Marlborough Sounds.

INTRODUCTION

The impact of spatial and temporal scales on the feeding and development of mussels has been emphasised in Section 2.1. It is now necessary to understand which factors affected the vitality of mussels at these different scales. Tentative identifications of environmental and community variables affecting the biology of *P. canaliculus* were made in Section 2.1. This study employs multivariate statistical methods to identify a range of factors which affect the nutrition and growth of *P. canaliculus* within the intensive mariculture systems studied in the previous section.

At the start of my study, pigment assay was regarded as the best method for

determining feeding by herbivorous planktivores in the field (Baars and Helling 1985). However, recent research suggests that pigment assay may underestimate feeding (Conover et al. 1986; Hawkins et al. 1986; Wang and Conover 1986). During this study, both pigment and inorganic tracers are used to calculate feeding rates for mussels. The study identifies the tracer which explains most variation in feeding, and assessed whether this tracer provided reliable estimates of the feeding of the mussel.

Feeding and energy uptake are determined within multiple response situations occurring within mussel farms using this tracer. The study attempts to identify a range of factors associated with changes in feeding behaviour. This range of factors may determine the dynamics of nutritive processes within mussel farms.

METHODS

The data set, described in Section 2.1, included the following factors: salinity (ppt), Secchi Disk transparency (m), temperature (^{o}C), wave height (cm). Biotic conditions were defined using mussel length (mm), drained weight and dry meat weight of mussels (g), condition index ([dry meat weight*100/drained weight]%), growth density ($n\ m^{-1}$) and an index of crowding. Food resources and feeding were described using chloropigments contained in water and faeces (ug), particulate inorganic matter in water and faeces (PIM: mg), and organic matter in water and faeces (POM: mg). Turbidity (m^{-1}) is defined as the reciprocal of Secchi disk transparency. The data included 113 cases collected from October, 1983, to September, 1984 (Appendix I). These included 71 cases collected within Crail Bay. Thus, this analysis is weighted, and may emphasise interactions occurring within mussel farms in Crail Bay.

Feeding rates were determined by assuming that chloropigment, and then PIM was an "inert" tracer. First, gut passage time was derived from temperature relationships determined in Section 3.2.2. Filtration rate, ingested ration and assimilation efficiency were then calculated using Equations 1 to 3. All equations assume that tracer was not assimilated, degraded or otherwise lost prior to the assay of faeces (Section 2.1).

$$F = \frac{F_t}{T_d * S_t} \qquad (1)$$

$$I = F * 24 * S_0 \qquad (2)$$

$$AE = 1 - \frac{F_0 * S_t}{F_t * S_0} \qquad (3)$$

where F is filtration rate (l h^{-1}), I is ingestion rate (g d^{-1}), AE is assimilation efficiency, F_t is tracer content of faeces (g), T_d is gut passage time (h), F_o is organic content of faeces (g), S_t is the mass of particulate tracer in seawater (g l^{-1}) and S_o is mass of organic matter present in seawater (POM, g l^{-1}).

All samples of faeces were then examined using a light microscope to determine whether dominant planktonic foods were digested efficiently.

Tracer Stability

Either PIM or chloropigment may be lost from food after filtration, and loss of a tracer will cause feeding to be underestimated when that tracer is used to determine feeding rates using Equations 1-3. Conover et al. (1986) compared the ratio of PIM:pigment in food and faeces to test the hypothesis that chloropigment was either assimilated from, or degraded within the gut. If either tracer were lost then lower proportions of that tracer will occur in faeces than occurs in food.

In the present study, the relative stability of the two tracers was tested by comparing the ratios of PIM:pigment before and after digestion of food. While food contained 3.5 $\pm$0.5 mg PIM for every micro-gram of chlorophyll, faeces contained only 0.9 $\pm$0.2 mg PIM per unit chlorophyll. As variances were unequal, a Kruskall-Wallis test was used to test the null hypothesis that equal proportions of PIM and pigment were found in food and faeces. The test indicated that lower proportions of PIM occurred in faeces than in food ($p<0.001$). Thus, PIM was probably rejected or otherwise lost ~~lost~~ from food, and use of PIM as an "inert" tracer can underestimate feeding rate and digestive efficiency in mussels.

No loss of pigment was detected during my study of *P. canaliculus*, and pigment tracers provided stable estimates of feeding. Unless otherwise stated, results of chloropigment assays are therefore used to describe feeding in the analyses presented below.

Bivariate Relationships

This data set was subjected to preliminary analysis to identify simple bivariate relationships between pairs of variables, and to identify non-linear associations that occurred between variables. The non-linear trends detected were removed by either transformation, or subdivision of data into two subsets which described feeding at high (>1.5 ug chlorophyll l^{-1}) and low food concentrations, respectively.

Multivariate Analysis

The following groups of independent variables were used in both regression

analysis of feeding and dry weight condition index, and in discriminant analysis of condition index:

1) environmental factors (salinity, temperature, turbidity, wave height),
2) food resource descriptors (chlorophyll, TPM, PIM, POM, PIM:TPM ratio),
3) descriptors of mussels (length, dry meat weight, condition index), and
4) descriptors of the mussel community (growth density, crowding index).

Volumes of water filtered by the mussels living on one metre of culture rope were also calculated by multiplying filtration rate (determined using pigment analysis) by the growth density of mussels (n m^{-1}), and this factor was used as an independent variable in analyses of condition index. Where a variable listed above was not included in tabulated results, either that variable did not contribute a significant linear term to the solution or the factor was excluded to reduce effects of multiple co-linearity (below).

Linear regression equations were determined using an All Possible Subsets algorithm (BMDP9R) to define optimal subsets of independent variables (Tables 1 and 2; Equation 4) using Mallows C_p to identify a subset of independent variables which explained most variation in, and were statistically associated with changes in the following dependent variables:

1) chloropigment content of faeces,
2) filtration rates of mussels,
3) ration ingested by mussels, and
4) efficiencies at which organic matter was assimilated from food, and
5) condition index of mussels.

Stepwise Discriminant Analysis (BMDP7M) was then used to classify mussels into three groups showing low (<8%), medium (8-10%) and high condition index (>10%), respectively. These classes were arbitrarily defined to create groups of similar size. The algorithm used a critical F value of 4.0 (df>67) to determine whether that independent variable having the greatest "F" value should be entered into the analysis. If entering additional variables into the model reduced the F value of a previously entered variable below 4.0, then that variable was removed from the model.

Thus, the number and order of entry of independent variables used in both regression analysis and discriminant analyses was determined by statistical evaluation, not by experimenter inference of independent variables. However, cross-correlated independent variables may induce multiple co-linearity (Sokal and Rohlf 1981). Co-linearity was reduced by excluding inter-correlated variables which described least variance of a dependent variable if an F test indicated that that term was not highly significant. If cross-correlated variables could not be excluded from an analysis, path analysis (Sokal and Rohlf 1981) was used to estimate the impact of cross-correlated independent variables upon a solution. Multivariate normal distribution was tested for

using both inspections of residuals and detrended normality plots of residuals. No violation of the regression assumption of multivariate normal distribution was found.

The proportion of variance explained by each regression equation is expressed as adjusted R^2 values, and the proportion of variance explained by each term within an equation is expressed as delta R^2. The F test was used to test the significance of all independent variables used in either regression equations or discriminant analyses.

RESULTS

Bivariate Feeding Relationships

As plankton chlorophyll increased from 0.3 to approximately 1.4 ug l^{-1}, the quantity of chloropigment recovered from faeces increased notably (Fig 1). Further inspection of points clustered around the upper bounds of the distribution in Figure 1 suggested that faecal pigment recovered from mussels of 80 to 95mm length was maximal above a threshold of 1.3-1.6 ug l^{-1} plankton chlorophyll. In 80-95mm length mussels, faecal pigment content (FCC) increased from 7ug chlorophyll equivalent at concentrations of 0.35 ug l^{-1} chlorophyll to a maximum of 60ug pigment in excess of 1.5 ug l^{-1} plankton chlorophyll (Fig 1). Thus, faecal pigment increased nine-fold as food concentration increased four-fold.

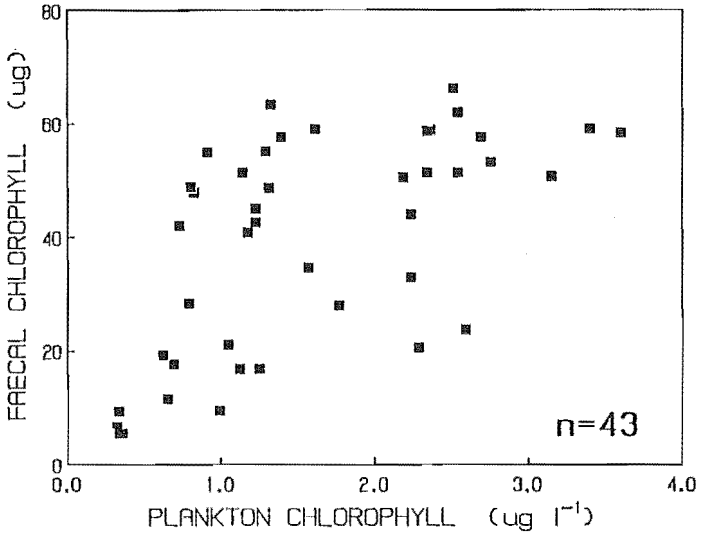

Figure 1. Effect of food concentration on faecal pigment content in mussels of 80-95mm length.

To detect the food concentration threshold at which this change in faecal pigment occurred, a reiterative regression procedure was used to measure how much variance in FCC was explained by subdividing data at different food thresholds. All data was subdivided into two groups describing feeding at high and low food concentrations. The thresholds at which data was subdivided were then increased from 1.0 to 2.0 ug $^{-1}$ plankton chlorophyll in 0.1 ug l^{-1} increments. This analysis indicated that maximal proportions of variance in FCC were explained after sub-dividing data at thresholds of 1.3-1.6 ug l^{-1} chlorophyll in mussels of 30 to 150mm length. After data was divided at 1.3 ug l^{-1} plankton chlorophyll to create groups of equal size, ANCOVA indicated that the decline in FCC at food concentrations below this cutpoint had a significantly different linear trend to that fitted for mussels feeding at higher food concentrations ($F=20.95$, $df=1$, $p=0.0004$). Therefore, two distinct phases of feeding behaviour were separated between chlorophyll *a* concentrations of 0.3 and 4.2 ug l^{-1} (0.4-5 mgC l^{-1} food). These different behaviours were analysed by sub-dividing data at an intermediate threshold of 1.5 ug l^{-1} plankton chlorophyll, and deriving two series of regression equations describing feeding in food poor and food rich waters, respectively.

While FCC increased exponentially with mussel length and an exponent of 3.51 explained most variance in FCC, use of different exponents to transform mussel lengths indicated that the fitting of curves was not particularly sensitive to the value of the exponent used. During laboratory studies, a length exponent of 3.01 was determined which described changes in ingestion rate with mussel length ($r^2=0.99$, Section 3.3.1) and transformation of lengths of mussels sampled in the field using the field exponent of 3.51 created strong linear trends within the bivariate plots of FCC against mussel length.

Both food concentrations occurring within an embayment, and local depletion of food may determine the availability of food in the proximity of culture ropes. When log plankton chlorophyll was plotted against log faecal chloropigment (Fig 2), most cases recorded above 1.5 ug l^{-1} plankton chlorophyll plotted in an elliptic cluster that probably represents mussels having a maximal gut content. In contrast, mussels sampled at less than 1.5 ug l^{-1} plankton chlorophyll frequently showed reduced faecal chlorophyll compared with mussels sampled at higher food concentrations. Amongst the factors which may have caused this reduction in FCC are (1) low concentrations of food entering the farm, and (2) reduction of food concentration near actively feeding mussels.

If faecal pigment had declined only at low food levels then FCC should become more strongly correlated with mussel length above 1.5 ug l^{-1} chlorophyll, and less scatter did occur around a regression line describing variation in FCC above ($r^2=0.47$), rather than below this threshold ($r^2=0.25$, data shown in Fig 2). However, the strongest bivariate relationship between mussel length and FCC was not found until all mussels feeding at below 2.2 ug l^{-1} plankton chlorophyll were excluded from analyses. This

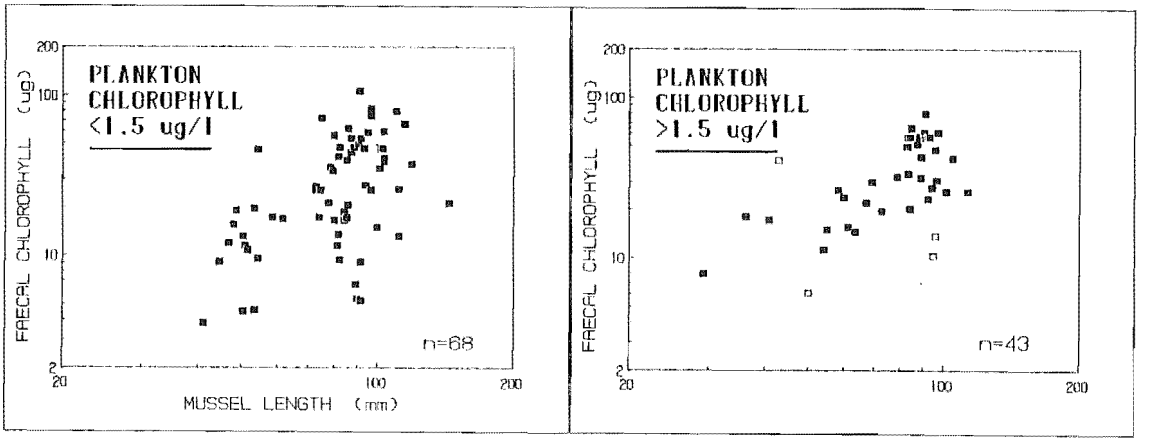

Figure 2. Effect of mussel size on faecal pigment content above and below a food concentration threshold of 1.5 ug l^{-1} chlorophyll a. Four points marked with open squares (right) represent statistical outliers identified during regression analysis.

food concentration was substantially higher than the feeding threshold at which 80-95mm length (above) and 30-120mm length (multivariate analysis, below) ingested their maximal ration. In some instances, therefore, the feeding of mussels probably depleted food resources occurring between culture ropes. This source of food depletion was not determined by measurements of food resources occurring one metre from culture ropes, and the additional factor may explain why some mussels attained maximal FCC at a higher food concentration than indicated by earlier estimates of the feeding threshold.

The Multiple Response Situation

Faecal Chloropigment Content (FCC)

The subdivision of data at a threshold of 1.5 ug l^{-1} chlorophyll increased the proportion of variance explained by regression analysis of faecal pigment from 45% (all data), to 74% at low food concentrations and 68% at high food concentrations. Analysis of regression coefficients obtained for the independent variable plankton chlorophyll indicated that the slopes of curves obtained above and below this food threshold, respectively, differed markedly ($T=2.51$, $df=111$, $p=0.007$). As ANCOVA using data presented in Figure 1 (above) also showed differences in faecal pigment above and below a similar threshold (1.3 ug l^{-1} plankton chlorophyll, $p=0.0004$), two different feeding behaviours probably occurred at high and low food concentration, respectively.

At low food concentrations, FCC increased most markedly with both shell length ($R^2=0.49$, $p<0.001$) and food concentration (plankton chlorophyll: $R^2=0.16$, $p<0.001$, Table 1). Whereas temperature and turbidity were also weakly associated with faecal pigment

FOOD CONCENTRATION

LOW HIGH

FAECAL PIGMENT CONTENT

VARIABLE (Base Unit)	COEFFICIENT	P	R^2	VARIABLE (Base Unit)	COEFFICIENT	P	R^2
Intercept (ug chl a)	-15.59	0.058		Intercept (ug chl a)	0.44	0.99	
Length Exp ($mm^{3.51}$)	$4.54*10^{-4}$	<0.001	0.49	Length Exp ($mm^{3.51}$)	$3.47*10^{-4}$	<0.001	0.31
Chlorophyll (ug l^{-1})	49.34	<0.001	0.16	PIM:TPM (ratio)	-84.10	0.001	0.20
Temperature (°C)	-2.86	0.023	0.06	Temperature (°C)	-4.19	0.001	0.17
Turbidity (m^{-1})	166.15	0.072	0.03	Salinity (ppt)	3.44	0.06	0.06

FILTRATION RATE

VARIABLE (Base Unit)	COEFFICIENT	P	R^2	VARIABLE (Base Unit)	COEFFICIENT	P	R^2
Intercept ($l\ h^{-1}$)	-30.82	0.001		Intercept ($l\ h^{-1}$)	-1.29	0.74	
Length Exp ($mm^{3.51}$)	$0.89*10^{-5}$	<0.001	0.59	Temperature (°C)	1.42	<0.001	0.49
Temperature (°C)	1.80	<0.001	0.16	POM (mg l^{-1})	-3.95	0.007	0.13
Wave Height (cm)	-0.04	0.001	0.06	Length Exp ($mm^{3.51}$)	$0.18*10^{-6}$	0.010	0.10
Gut Passage Time (h)	0.94	0.011	0.04	Chlorophyll (ug l^{-1})	-1.54	0.082	0.05
POM (mg l^{-1})	2.58	0.036	0.02	Growth Dens ($N\ m^{-1}$)	-0.007	0.098	0.04

INGESTION RATE

VARIABLE (Base Unit)	COEFFICIENT	P	R^2	VARIABLE (Base Unit)	COEFFICIENT	P	R^2
Intercept (gC d^{-1})	0.21	0.84		Intercept (gC d^{-1})	-8.30	<0.001	
Length Exp ($mm^{3.51}$)	$3.76*10^{-5}$	<0.001	0.49	Temperature (°C)	0.67	<0.001	0.53
Chlorophyll (ug l^{-1})	1.87	0.02	0.13	Length Exp ($mm^{3.51}$)	$3.24*10^{-5}$	0.007	0.15
Gut Passage Time (h)	-0.27	0.04	0.09				

Table 1. Statistics describing variation in faecal pigment (top), filtration rate (middle) and ingestion rate (bottom), at food concentrations exceeding (right) and below (left) a threshold of 1.5 ug l^{-1} chlorophyll.

content ($p<0.07$), increased length and food alone accounted for 61% of the 74% variance explained by this equation.

At high food concentrations, faecal pigment also increased markedly with mussel length ($R^2=0.31$, $p<0.001$, Table 1), but did not vary with food concentration at chlorophyll concentrations above 1.5 ug l^{-1}. The formation of this plateau representing maximal gut content was consistent with the hypothesis that mussels' feeding became satiated at high food concentrations. FCC also fell as increased proportions of inorganic matter occurred in the food resource ($R^2=0.20$, $p=0.001$). Therefore, ingestion of particulate inorganic matter may exclude food containing plant pigment from diets of mussels. The sample indicated that faecal pigment declined with temperature ($R^2=0.17$,

p=0.001), but path analysis indicated that covariance of temperature with the ratio PIM:TPM may induce this apparent association. Whereas faecal pigment could also decline with salinity (p=0.06), this solution may also result due to covariance.

Filtration Rate

Estimates of filtration rates were strongly dependent on the faecal tracer used to determine gut content (Kruskall-Wallis test, $p<0.001$), and the two methods produced markedly different results. When filtration rate was calculated using inorganic "ash" markers, 70% of mussels of 70-100 mm length apparently filtered less than 2 l h^{-1}, and slow rates were therefore recorded at low food concentrations when maximal filtration was expected (Section 3.2). When filtration rate was calculated using pigment markers, 90% of mussels of 70-100 mm length filtered from 2 to 14 l h^{-1}, a range similar to that recorded in subsequent experiments (Section 3). As PIM had been shown to be lost prior to assay of PIM in faeces, filtration was therefore determined using chloropigment as an inert tracer.

The equations used to determine filtration rate (Eqns 1 and 2) used both gut passage time and chlorophyll *a* concentration, and this rate is therefore correlated with plankton chlorophyll, gut passage time and, indirectly, with temperature. Chlorophyll was excluded from this analysis to reduce effects of cross-correlation on the equation. However, both temperature and gut passage time may affect feeding markedly, and neither factor was excluded from regression analyses. Equations describing filtration rate may not necessarily, therefore, include these two variables due to a natural dependence between filtration, and either temperature or gut passage time.

Filtration was both maximal and independent of food concentration below 1.5 ug l^{-1} plankton chlorophyll *a*. At these low food concentrations, 79% of variance in filtration was explained by environmental change and variation in mussel length (Table 1, $p<0.0001$). Filtration increased rapidly with both mussel length ($R^2=0.59$, $p<0.001$) and temperature ($R^2=0.16$, $p<0.001$). The temperature dependent variable gut passage time also explained additional variance to that accounted for by temperature alone ($R^2=0.04$, $p=0.01$), and simple cross-correlation with temperature did not explain this result as gut passage time was entered into the regression after water temperature. Filtration may also both increase slowly as food concentration increases (POM: $R^2=0.02$) and decline during strong wave action ($R^2=0.06$), however, path analysis indicated that these relationships could also result from cross-correlation with water temperature. While reduction of filtration during intense wave action is plausible, it was not therefore shown to occur.

Above 1.5 ug l^{-1} chlorophyll, filtration declined markedly as food concentrations increased ($p=0.01$). The regression equation suggested that filtration by 80 mm long

mussels declined from 9.1 to 0.5 l h^{-1} as food increased from 1.5 to 3 ug l^{-1} chlorophyll (2-4 mg l^{-1} POM). However, as chloropigment rejected in pseudofaeces was not measured by the technique used to determine filtration rate, this equation may overestimate the rate at which filtration declined as food increased. Filtration also increased markedly with temperature ($p<0.001$), and less rapidly with mussel length ($p=0.01$). The dependence of filtration on mussel length was, however, less marked than at low food concentrations and this equation may emphasise the impact of temperature on filtration and under-emphasise effects of mussel size on filtration rate.

Ingested Ration

At low food concentrations only three factors affected ingestion significantly, but these factors collectively explained 64% variance in ration ($p<0.0001$). Ingestion increased most markedly with shell length ($R^2=0.49$, $p<0.001$), and also increased notably with both food concentration ($R^2=0.13$, $p=0.02$) and water temperature ($R^2=0.09$, $p=0.04$).

At high food concentrations, ingestion rate was not associated with any measure of food concentration. Ingestion was enhanced significantly by increases in both temperature ($R^2=0.53$, $p<0.001$) and shell length ($R^2= 0.15$, $p<0.01$), and these two factors collectively explained 62% variance in ingestion rate ($p<0.001$).

Assimilation efficiency

Two methods were used to calculate assimilation efficiency (AE). AE was determined using both "ash" (Conover 1966) and chloropigment (Downs and Lorenzen 1985; Landry et al. 1984) as tracers, and these techniques produced different results (Kruskall-Wallis test, $p<0.001$). This is not surprising as initial trials indicated that PIM was rejected in pseudofaeces or lost from food prior to collection of faeces.

Assay of ash suggested that a mean of only 30% $\pm$7% of the carbon ingested in food was assimilated ($n=50$), but AE determined using this method was variable and ranged from -32% to 86%. Negative assimilation was determined in 10 cases, indicating that the use of ash tracers can underestimate AE. Such a result may arise due to secretion of metabolic carbon into faeces (Bayne et al 1987), except in that case estimates of AE made using pigment as tracers (below) should decline also. This did not occur. My estimates, however, indicated that mussels took up 2.5% $\pm$1.2% body C d^{-1}. As *P. canaliculus* can grow by 1.8% C d^{-1} (data: Section 2.1), a net growth efficiency exceeding 70% is therefore needed to support somatic growth alone, and this estimate of energy uptake determined using "ash" tracers was below the energy uptake required to sustain the total costs of somatic growth, gametogenesis plus respiration.

In contrast, when AE was determined by pigment assay, in 88% of mussels AE exceeded 60% and, on average, 81 $\pm$5% of the carbon ingested as food was assimilated.

Mussels were estimated to take up 11.7% $\pm$3.7% body C d^{-1}, and this energy uptake could support both somatic growth of 1.8% C d^{-1} and additional energy dependent metabolic processes. As this growth rate does not include gamete production, net growth efficiency probably exceeded a minimal value of 15% of the energy taken up by *P. canaliculus*.

Microscopic examination of foods and faeces also indicated that foods comprising this mixed and natural food resource were digested efficiently. The majority of foods were degraded beyond recognition. Few species of phytoplankton were voided intact, and these cells represented a small fraction of the POM. Thus, microscopy indicated that the higher estimates of assimilation calculated using pigment assay may be more dependable, and these estimates of assimilation efficiency were used to formulate the following regression equation:

$$AE = 97.24 - 1.21\ T \qquad [p<0.001] \qquad (4)$$

where AE is assimilation efficiency (%) and T is temperature (^{o}C).

Regression analysis indicated that temperature was the only factor which affected assimilation efficiency ($p<0.01$), and suggested that AE declined from 85% at 11^{o}C in winter to 75% at 18^{o}C during summer. The actual factor causing this moderate change may be seasonal in nature, and such factors include temperature alone, change in the digestibility of ingested foods, or minor microbial loss of faecal carbon prior to determination of AE. It is noteworthy, however, that digestive efficiency did not vary with either shell length, food concentration or ingestion rate ($p>>0.05$), and AE was only weakly dependent on temperature. Thus, this analysis indicated that energy uptake was not strongly dependent on any of the factors studied.

Condition Index

Regression analysis of 113 cases from all embayments explained only 23% of the variance in condition index, whereas analysis of 71 cases from Crail Bay explained over 51% variance in condition. The reason that more variance was explained in Crail Bay may be that some critical factor that varied between embayments (eg current speed) was not measured, and a regression analysis of changes in condition within Crail Bay is presented in Table 2.

In Crail Bay, condition increased with shell length at all concentrations of food, and in all analyses (Table 2, $p<0.003$). Below 1.5 ug l^{-1} chlorophyll, condition declined as temperature increased ($p<0.001$), and within dense communities clearing more water of food ($p=0.01$). Above 1.5 ug l^{-1} chlorophyll, condition declined in turbid water containing large fractions of PIM ($r^2=0.33$, $p<0.001$). Condition also declined when

LOW FOOD CONCENTRATION (chlorophyll <1.5 ug l^{-1})				
VARIABLE	(Base Unit)	COEFFICIENT	P	R^2
Intercept	(%)	13.11	<0.001	
Temperature	(°C)	-0.46	<0.001	0.20
Mussel Length	(mm)	0.05	<0.001	0.20
Volume Filtered	(l)	-0.00011	0.013	0.07
Overall Regression: n=46, p<0.0001, r^2=0.51				

HIGH FOOD CONCENTRATION (chlorophyll >1.5 ug l^{-1})				
VARIABLE	(Base Unit)	COEFFICIENT	P	R^2
Intercept	(%)	10.68	<0.001	
Turbidity	(m^{-1})	-27.07	<0.001	0.33
Chlorophyll	(ug l^{-1})	-1.15	0.002	0.20
Mussel Length	(mm)	0.05	0.003	0.20
Overall Regression: n=25, p=0.0001, r^2=0.59				

Table 2. Regression statistics describing variation in the condition of mussels.

Table 3. Classifications of mussels into groups of different condition index using abiotic and biotic data (discriminant analysis).

[A] ALL EMBAYMENTS

STEP	VARIABLE (IN/OUT)	F TO ENTER OR REMOVE	NUMBER OF VARIABLES	APPROXIMATE " F "	df	p
1	Mussel Length	6.61	1	6.61	110	<0.03
2	Volume Filtered	9.94	2	8.22	218	<0.01
3	Mussel Crowding Index	4.18	3	7.00	216	<0.01

CONDITION INDEX GROUP	PERCENT CORRECTLY CLASSIFIED	NUMBER OF CASES PLACED IN GROUP: 6.5-8.0	8.0-9.9	10.0-12.6
6.5-8.0	67.6	23	5	6
8.0-9.9	44.4	10	16	10
10.0-12.6	69.8	7	6	30

[B] CRAIL BAY

STEP	VARIABLE (IN/OUT)	F TO ENTER OR REMOVE	NUMBER OF VARIABLES	APPROXIMATE " F "	df	p
1	Temperature (in)	8.83	1	8.82	68	<0.01
2	Mussel Length	7.70	2	8.19	134	<0.01
3	Volume Filtered	4.79	3	7.30	132	<0.01
4	Temperature (out)	3.36	2	9.01	134	<0.01

CONDITION INDEX GROUP	PERCENT CORRECTLY CLASSIFIED	NUMBER OF CASES PLACED IN GROUP: 6.5-8.0	8.0-9.9	10.0-12.6
6.5-8.0	71.4	10	2	2
8.0-9.9	39.1	6	9	8
10.0-12.6	70.6	4	6	24

chlorophyll concentration exceeded 1.5 ug l^{-1} ($p=0.002$), and no reason for this decline was apparent from the feeding data collected.

Stepwise discriminant analysis was then used to determine a range of independent variables which may give rise to a high condition index. This indicated that water temperature, mussel length, growth density, and volumes of water cleared of food by a mussel farm community could be used to predict condition in 71% of cases. These four factors may be useful in defining environments which could support mussels of high condition.

Separate analyses were conducted using (1) data collected from all embayments, and (2) data from Crail Bay alone. Both analyses indicated that high condition was associated with mussels of larger size, and that low condition was associated with high rates of clearance of water of food (Table 3). The index of crowding was only a significant predictor of condition in the analysis of data from all embayments, and this was probably due to high stock densities recorded in embayments other than Crail Bay. In Crail Bay, while temperature was the first predictor of condition used in the analysis, temperature was removed after both mussel length and the volume of water cleared of food were included in the model. Whereas this association of low condition and high temperature can also be attributed to interaction between length and clearance of food, the volume of water cleared of food was temperature dependent. After the volume of water cleared of food was omitted from the analysis, it terminated at Step 2 and temperature was identified as an important determinant of condition index.

DISCUSSION

This study indicates that *P. canaliculus* ingests a maximal, or near maximal ration in most of the situations studied. Of the 14 variables tested, only three were associated with reduced food intake. Temperature and mussel size affected rates of feeding at all food concentrations, and an interesting threshold feeding behaviour also limited filtration at high food concentrations. These three factors controlled ingestion rate, and most foods were digested efficiently. Mussels apparently exploited their food resources efficiently. However, before these statements can be accepted, the validity of using pigment tracers to determine feeding rates and digestive efficiency must be evaluated.

Analysis using dietary chloropigments (Shuman and Lorenzen 1975) may provide the best "*in situ*" technique for measuring feeding (Baars and Helling 1985). Convincing estimates of feeding have been derived using chloropigment tracers (Nicholajsen et al. 1983; Welschmeyer and Lorenzen 1985; Helling and Baars 1985), but error may result from loss of pigment tracer within the gut (Hawkins et al. 1986; Wang and Conover 1986;

Conover et al. 1986). This criticism had unknown relevance to my study, and was assessed prior to analysis of feeding behaviour.

After exposing mussel faeces to sunlight for 48 hours an atypical absorption band was found at 683nm (unreported trial), the wavelength of an absorption maxima of protochlorophyllide *a* (Goodwin 1976). Whereas occurrence of this band may indicate that pigment degradation occurs, the band was not present in faeces of mussels collected during my study, and the available absorption spectra do not suggest that significant degradation of pigment occurred.

Hawkins et al. (1986) used particulate inorganic matter (PIM) as an inert tracer to detect loss of chloropigment, and infer from increased ratios of PIM to chloropigment that pigment was lost from food in transit through the gut. However, secretion of PIM into the digestive tract (Bjorndal 1985) can also explain this change.

While I did not test the hypothesis that pigment was lost from the gut, the assumption that neither pigment nor PIM were lost is tested. If true, then the ratio PIM:pigment would be similar in food and faeces, but faeces contained only 26% of the PIM per unit pigment contained in food ($p<0.001$), indicating either that PIM was lost from filtered food or more pigment was defaecated than ingested. I know no source of chloropigment that is not associated with PIM in food, and loss of PIM occurs which can cause underestimation of feeding using PIM tracers. It is notable that energy uptake calculated from PIM is insufficient to support the growth of cultured mussels, and this also suggests that PIM was not an inert tracer. However, whereas PIM may be lost from the gut or faeces, my data could also be explained by differential rejection of silt in pseudofaeces (see Kiorboe et al. 1980), and loss of PIM may not occur after ingestion. Specifically, relatively more silt particles may have been rejected at the labial palps than were eaten by the mussel.

Wang and Conover (1986) compared results of grazing studies with feeding rates determined using fluorometric assay of pigment, and found the proportion of pigment recovered from guts of copepods declined from 80% to 6% as ingestion rate declined. Low food levels used by Hawkins et al. (1986) and Conover et al. (1986) could therefore cause the marked pigment loss they record. Substantially less chloropigment may be lost by animals fed at high concentrations of food (Conover et al. 1986). Kleppel et al. (1988) therefore argue that pigment assay provides good estimates of feeding, a conclusion supported by comparison of the natural feeding of *Centropages hamatus* with its feeding in the laboratory (Nicholajsen et al. 1983), and analysis of sources of variability of gut fluorescence in other copepods (Ohman 1988). Comparisons of feeding by *P. canaliculus* between field and laboratory situations also indicated that pigment assay provided reasonable estimates of the feeding of mussels filtering at moderate to high concentrations of food (Section 4).

Mussel Feeding

There has been general agreement in the literature that filtration and ingestion rates increase with the size of mussels (*M. edulis*: Thompson and Bayne 1974; Widdows 1978; Sprung 1984b; *M. chiliensis*: Navarro and Winter 1982) and as temperature increased to 20°C (*M. edulis*: Walne 1972; Wilson and Seed 1974; Schulte 1975; Walz 1978; Sprung 1984b). Similar trends also occurred in *P. canaliculus*.

Controversy exists, however, as to how feeding behaviour is affected by increased food concentration. While some studies suggest that filtration rate is maximal over a wide range of food concentration (see Thompson and Bayne 1974; Widdows 1978; Thompson 1984), others indicate that filtration was high below 1 mgC l^{-1} food, but declined markedly at food concentrations exceeding a lower threshold (eg Winter 1973; Winter 1978a; Navarro and Winter 1978; Sprung 1984b). Both behaviours have been recorded in *M. edulis*, and do not simply reflect interspecific variation.

It is therefore interesting to establish how *P. canaliculus* feeds so that its feeding behaviour in the field can be compared with that of this (Section 3) and other mussels in experimental systems. My study found a distinct feeding threshold at 1.3-1.5 ug l^{-1} chlorophyll *a* (approximately 1.4-1.8 mgC l^{-1} food). Below food threshold, rapid filtration occurred while ingestion was food limited (Fig 3). Above the threshold filtration rate declined as food concentrations rose, and maximal and constant rations of food were eaten. This behaviour therefore resembled threshold feeding recorded during studies on *M. chiliensis* (Navarro and Winter 1982), *M. edulis* (Winter 1973; Sprung 1984b) and other bivalves (eg Winter 1969; Walz 1978; Epifanio 1981; Gerdes 1983).

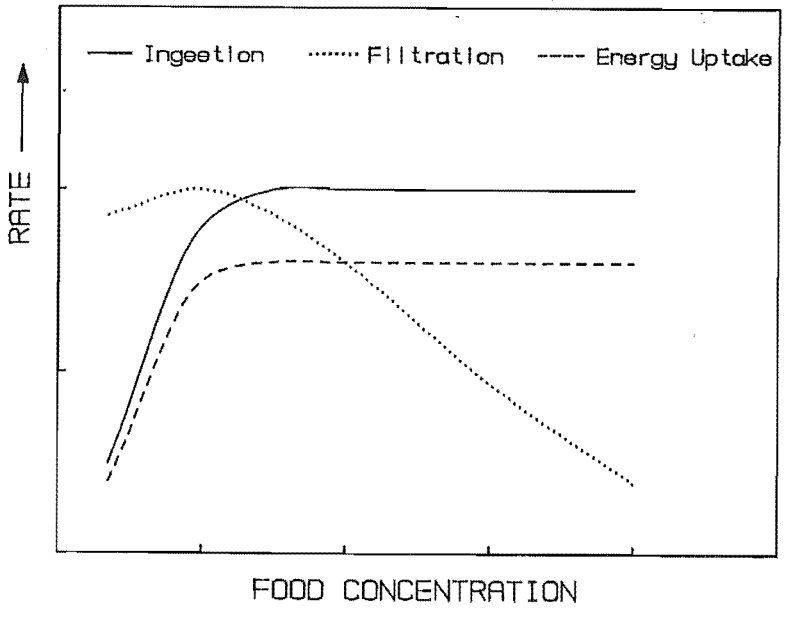

Figure 3. Feeding and nutrition of P. canaliculus *in relation to food concentration: models derived using regression analysis.*

Threshold feeding probably has ecological significance.

Firstly, if this threshold of 1.3-1.5 ug l^{-1} chlorophyll occurs within the range of food concentrations recorded within any region, then filtration, ingestion and energy uptake is predicted to vary both between sites and over time. Chlorophyll concentrations varied from 0.3 to 13.0 ug l^{-1} in the Kenepuru and Pelorus Sounds (Mackenzie et al. 1986; Bradford and Chang 1987; Bradford et al. 1987; Hickman et al. in prep; this study), from 0.2 to 4.0 ug l^{-1} in adjacent waters (Bradford et al. 1986) and from of 0.5-11.0 ug l^{-1} in other areas (Bricelj et al. 1987; Page and Hubbard 1987). This threshold concentration therefore occurs within the ranges of food sampled both in Marlborough, and in other areas. Marked spatial and temporal variation occurred in feeding and development of *P. canaliculus* in Marlborough, and such variation may also occur in different areas characterised by similar fluctuations of food concentration.

Secondly, feeding by dense colonies of farmed (Cabanas et al. 1979; Rosenberg and Loo 1983; Rodhouse et al. 1985; this study) and wild mussels (Frechette and Bourget 1985a) depleted water of food, and the magnitude of this reduction in food availability may vary with food concentration. Below the feeding threshold of 1.3-1.5 ug l^{-1} chlorophyll, 3-10 times more water was filtered than was filtered at higher food concentrations. Most water was filtered, and food depletion within mussel farms was therefore most intense, during those periods when low food concentrations present in an embayment already limited food intake by mussels. Maximal food depletion therefore occurred while mussels were sensitive to any further reduction of food concentration.

Finally, the size and distribution of mussels present within farms also affects the impact of filtration on food availability. Stock density varies 3-fold at any time, and is reduced 60% on reseeding mussels. Volumes of water cleared of food increase 50 times as mussels grow from 30mm length at reseeding, to 100mm at harvest. Such communities may therefore show capacities to deplete water of food which vary 3-fold between farms of similar structure, and 20-fold between reseeding and harvest of mussels. Maximal depletion of food is predicted to occur shortly before harvest.

This study indicated that filtration rate and food depletion were linked phenomena. Calculated filtration rates were maximal at both high temperature and low food concentration. Both conditions occurred between December and February when the greatest levels of food depletion occurred in the field (Section 2.1). Food depletion probably limited the food intake and condition of *P. canaliculus* (Section 2.1; this study), and limited growth by *M. edulis* (Frechette and Bourget 1985b). Improved understanding of food depletion and other factors that modify the food resource may therefore be required both to understand the dynamics of the nutritive process in *P. canaliculus*, and to optimise the structure of mussel farms in Marlborough.

The composition of the food resource can also affect feeding, as presence of silt

may either enhance energy uptake (Mohlenberg and Kiorboe 1981) or displace digestible foods from the diet (Kiorboe et al. 1980) and reduce assimilation and growth (Bayne et al. 1987) of *M. edulis*. In *P. canaliculus*, when inorganic matter comprised a large fraction of suspended particulate matter, phytoplankton was displaced from the diet at high food concentrations. At high food concentrations, a maximum volume of food was ingested, and consumption of refractory PIM at this time may reduce the quantity of organic material that can be digested. It is notable that mussel condition also declined when turbidity was high and food resources included most refractory matter (Table 2). PIM ingested at high food concentrations therefore may be detrimental to nutrition and growth. At low food concentrations, when mussels were unable to ingest a maximal ration, less digestible foods (PIM) did not displace readily digested foods from the diet. Organic matter associated with sediment may actually enhance nutrient uptake at low food levels. The ingestion of silt and poor quality food therefore probably exerts different effects on energy uptake and growth at different concentrations of food.

Bayne et al. (1987) suggest that assimilation efficiency declines markedly when sediment is present within the food resource. However, foods sampled during my study contained large fractions of organic matter similar to that contained in Diet 1 of Bayne et al. (1987). The high proportion of digestible matter present in the diet of *P. canaliculus* may explain why I found that digestive efficiency was not limited by the refractory matter occurring in the mussels diet.

Whereas many factors may affect the quantity of food digested, only water temperature showed a statistical association with changes in assimilation efficiency (Equation 4). Seasonal variation in foods may also induce changes in food quality that are correlated with temperature. Also, microbial breakdown of faecal carbon probably increases with increased temperature and, as preservation of faeces for later analysis occurred 36 h after defaecation, my study may underestimate carbon uptake. Thus, several factors may explain the weak association occurring between water temperature and digestive efficiency.

On average, determinations of faecal pigment indicated that 81% of the carbon contained in food was assimilated by *P. canaliculus*. This measure of AE is similar to the relatively high efficiencies of 79% (Cabanas et al. 1979), 80% (Rosenberg and Loo 1983) and 80% (Rodhouse et al. 1984) determined within other mussel mariculture systems. Similar high efficiencies obtained for *P. canaliculus* suggest that any breakdown of faecal carbon that did occur did not cause digestive efficiency to be underestimated markedly. My results therefore compare favourably with those obtained within other mussel farm communities.

These results generally indicate that the feeding of *P. canaliculus* in field

situations is influenced by a similar range of variables to the range which affects feeding in other bivalves. However, the value of these equations as predictive tools has not been evaluated. Whereas a plausible range of factors was identified which affected feeding, equations presented in Tables 1 and 2 should not be used as predictive models. The primary objective of this analysis was to identify those factors which induce variation in feeding, and one test of whether these factors were identified is to compare the major findings of this analysis with laboratory experiments describing feeding and energy flow in *P. canaliculus* (Section 3). Such comparisons are presented in Section 4.

Condition Index

The only factors which classified condition index using discriminant analysis were: (1) temperature, (2) mussel length, (3) volumes of water cleared of food, and (4) the index of crowding (Table 3). All these factors can be managed either through administration of the Marine Farming Act (1971) or by manipulating farm structures. Thus, my analysis suggests that management criteria can be developed to improve the condition of mussels produced in each farm, and to enhance product quality in the mussel farming industry.

Previous studies have suggested that different measures of the condition of *P. canaliculus* were affected by complex interactions of environmental factors such as the abundance of food, salinity and temperature (Flaws 1976; Hickman and Illingworth 1980; Hickman et al. in prep). I found two of these factors (food concentration and temperature) affected mussel condition.

While such factors may affect condition directly, spurious associations can also arise due to covariance. Similar sites were sampled by myself and Hickman et al. (in prep). Whereas condition was affected by feeding during my study, Hickman et al. identify food concentration or salinity as a control of mussel condition. However, they indicate that salinity may be defined as a determinant of condition due to its covariance with food concentration. Furthermore, whereas temperature may affect condition directly (Flaws 1976; Hickman and Illingworth 1980), changes in temperature dependent processes, such as the rate at which water was cleared of food, could explain this relationship between water temperature and mussel condition. Also, while the condition of *P. canaliculus* increased as mussels grew and matured (this study), condition did not increase with length in mature mussels exceeding 80mm length (Hickman et al. in prep). Maturity may therefore be the actual factor affecting condition. At present, the range of factors affecting this mussel's condition is not therefore well defined.

Feeding by *P. canaliculus* has not been measured previously, and my study is the first to examine how feeding affected condition. This study indicated that biotic factors such as the volume of inorganic matter in the diet, the rate of clearance of food

from water surrounding mussel communities and stock density can also affect condition. The study therefore provides the first indication that the structure and function of the mussel community exerts a direct influence on condition. However, while better understanding of biotic and nutritional inter-relationships occurring within mussel farm communities may promote greater understanding of factors regulating the growth and condition of *P. canaliculus*, this study does not indicate that a simple, linear association occurs between diet and condition.

Interrelationships of Food, Feeding and Development

In this study, temperature, food concentration and mussel size were dominant factors controlling filtration, ingestion and energy uptake by *P. canaliculus* in Marlborough. While presence of adequate food is the single most important factor regulating growth by mussels (Seed 1976), low food concentration probably limited energy uptake in only 30% of mussels sampled from Mills Bay, Schnapper Point, Four Fathom Bay and Crail Bay. Only in Richmond Bay were food concentrations sufficiently low (<1.3 ug l^{-1} chlorophyll) to limit energy uptake during more than 80% of the year, and mussels at this site had lower condition than at other sites (Hickman et al. in prep; Section 2.1). In addition, whereas food concentrations at the upcurrent edge of a farm in Crail Bay may only limit feeding for 30% of the year, within the farm sampled most intensively food may limit energy uptake during approximately 70% of the year. Mussels living within this farm in Crail Bay also showed lower shell length, condition and meat yield (Section 2.1). My analysis therefore indicated that feeding may become food limited most frequently, and most severely, at seaward sites in Marlborough and at downcurrent sites within mussel farms. Reduced growth also occurred at these sites. Agreement therefore exists between major conclusions of this regression analyses (during which statistical methods were used to determine the subset of predictor variables used) and the development of mussels within marine farms.

Of the environmental factors studied, food concentration, salinity and other factors seldom limited feeding at the upcurrent edges of most mussel farms. The notable absence of a marked and persistent limitation of feeding rate may explain rapid growth and high condition of *Perna canaliculus* reported from many regions of the Marlborough Sounds (Flaws 1976; Hickman 1979; Hickman and Illingworth 1980; Hickman et al. in prep; this study). The occurrence of food concentrations exceeding the minimal levels defined above may be an important factor determining the suitability of this area for mussel farming. The persistent presence of sufficient food may also prove to be a useful criteria for evaluating the potential of untried areas that are designated for the intensive culture of mussels.

SECTION 3.1.

A new, automated system for energetic studies illustrated by experiments on the impacts of selected internal and external stimuli on the feeding of mussels.

ABSTRACT

A laboratory system was constructed to regulate food supply, flow regime, temperature and salinity, and record feeding behaviour in controlled environments. Food concentration was regulated at 0.03-10.8 mgC l^{-1} over protracted periods (<4 d) while mussels fed in low turbulence flows of 5-28 cm s^{-1}. The new system allowed energy and oxygen uptake to be determined, and energy budgets to be calculated. Seven studies of mussel feeding are presented to demonstrate this new system.

Both internal and external factors affected filtration rate. At an oxygen concentration of 1.5 ppm O_2, filtration was only one tenth of that recorded at 5.0 ppm O_2. At 34 ppt salinity, mussels filtered 5.3 l h^{-1}. When salinity was rapidly reduced to 25 ppt filtration ceased, but recovered to 5.3 l h^{-1} 8 h after the salinity shock. Current speed did not affect feeding within the range 5-28 cm s^{-1}.

After 24 h food deprivation, feeding behaviour depended on the food concentration. After starvation, filtration increased by only 32% when mussels were supplied with 0.3 mgC l^{-1} food. However, when supplied with 1.5 mgC l^{-1} food after starvation, filtration peaked at twice the stable rates recorded 18 h later.

Following extrusion of sperm by males, mussels of both sexes ceased to feed. Filtration rates remained depressed until sperm were deliberately removed 17 h after sperm were extruded. Filtration by an unspawned population of mussels also declined by up to 81% in the presence of eggs.

INTRODUCTION

In laboratory systems, feeding by mussels (Riisgard and Randlov 1981; Sprung 1984) and other animals (see Stemberger 1986) has been shown to vary with time. Thus, long-term experiments may be needed to determine feeding in stable environments. These have been achieved using automated systems to control food supply to mussels over periods exceeding 24h (Riisgard and Randlov 1981; Navarro and Winter 1982). Modifications to Winter's (1973) feeding system have improved the precision of food

regulation at low concentrations (Riisgard and Mohlenberg 1979; Gallager and Mann 1980). However, neither of the two modified systems were versatile enough to conduct the integrated studies needed to determine "Scope for Growth".

An integrated system is presented in which food intake, assimilation and oxygen uptake were measured concurrently, allowing calculation of energy budgets. This system produces low-turbulence flows and contains traps to reduce breakage of faeces. This system was used to determine feeding rates (this study), and is later used to determine "Scope for Growth" under different conditions (this section).

Many factors such as temperature, food concentration and mussel size have been shown to influence feeding by mussels in the laboratory (Winter 1978; Navarro and Winter 1982; Sprung 1984a). Current speed may (Kirby-Smith 1972; Wildish and Kristmanson 1979) or may not (Riisgard and Mohlenberg 1979) affect feeding of bivalves. Salinity shock can also inhibit feeding by *M. edulis* (Widdows 1985), but this factor has not been evaluated for *P. canaliculus*. Whereas filtration by *M. edulis* declined below 100 mmHg O_2 (Bayne 1975), the role of oxygen in regulating feeding by *P. canaliculus* is not known. The impacts of food deprivation and experiment duration on filtration have not been investigated. Finally, while male *M. edulis* reduced their feeding rate after spawning, the presence of sperm did not affect feeding directly (Newell and Thompson 1984). Many factors mat therefore interact to determine feeding.

However, it is sometimes difficult to apply evaluations of factors from the literature to different populations of mussels growing in different environments. This present study determines the feeding responses of a single population of mussels grown in similar sub-tidal locations to variations in current speed, oxygen tension, salinity, feeding history, and the presence of gametes.

MATERIALS AND METHODS

The apparatus (Fig 1) consisted of a chamber housing mussels, a food sensor, algal dose control systems, and a data logger. Decreased algal concentration reduced the output from a fluorometer and triggered inoculation of algal culture. Feeding rates were calculated from rates of algal inoculation required to maintain a constant food concentration.

Aquatic Systems

The main chamber measured 600 X 180 X 180 mm. Two sections of 92 mm ID perspex were mounted in the main chamber. The first section (160 mm long) housed an Archimedes Screw and baffles to promote laminar flow. A variable speed drive unit

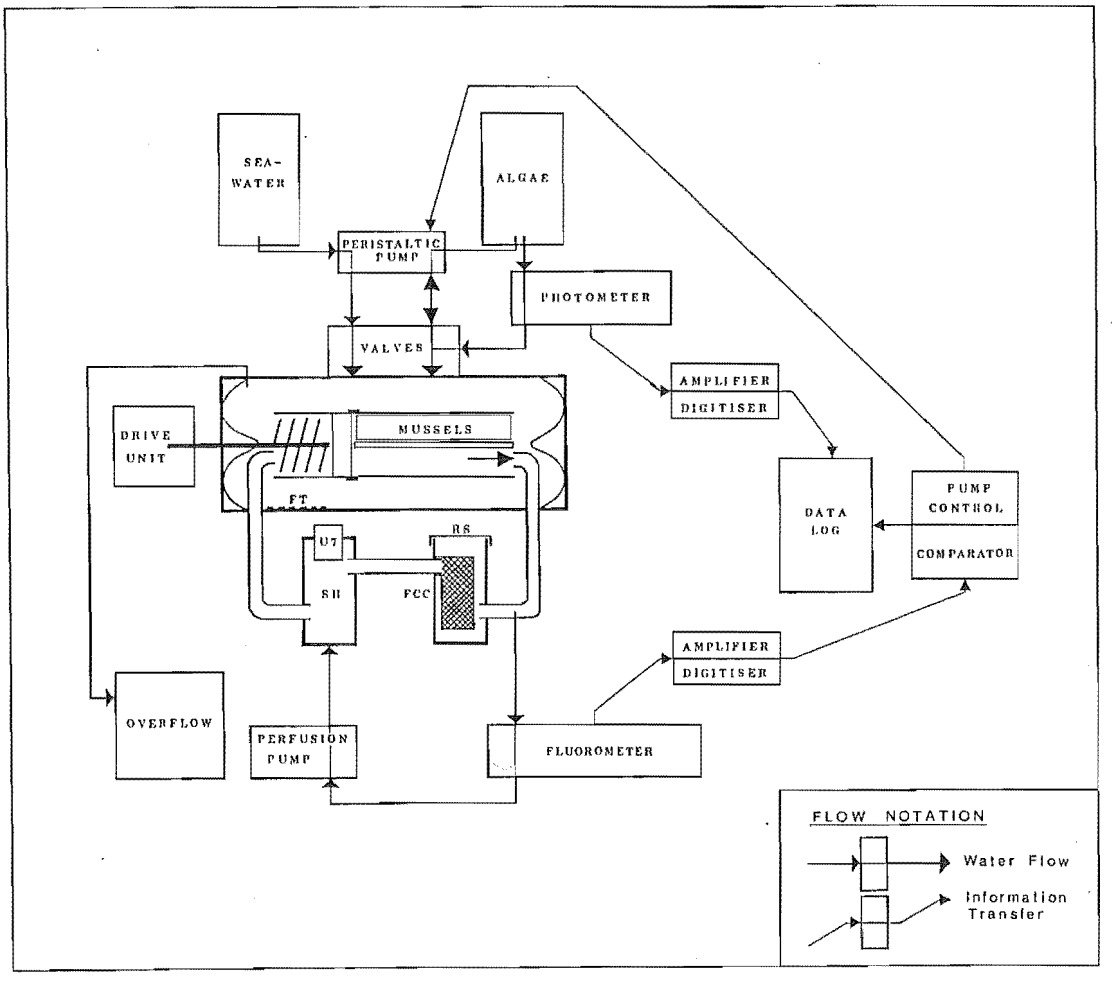

Figure 1. Schematic layout of the automated food regulation system used to measure feeding rates, and derive simple energy budgets of mussels. FT: faecal trap, U7: Horiba U-7 sensor, SH: sensor housing, FCC: faecal collection chamber, RS: removable seal.

drove the screw which produced flows of 5-104 cm s^{-1}. A detachable 310 mm section of perspex tube fitted into the first section of tube. Groups comprised of 6-30 mussels were supported on heavy duty plastic mesh which slotted into the top of this tube. Black plastic film screened these mussels from disturbance by the experimenter.

The system contained a total volume of 14.86 l of seawater.

Curved perspex mouldings guided water flowing out of the perspex tube round the end of the main chamber, reducing turbulence and faecal fragmentation. Faeces were transported into the main chamber and were collected in traps. At current speeds below 15 cm s^{-1}, faeces sedimented in a fluted trap located on the bottom of the main chamber. At higher flow rates faeces collected both in this trap and on 1 mm mesh bags in an adjacent chamber. The entrapment of faeces reduced disturbance of the food concentration sensor (fluorometer) by suspended faecal phytopigments, and provided sources of faecal matter from which assimilation efficiency was determined.

Water moved from the faecal collection chamber over the sensor of a Horiba U-7 or YSI Model 57 Oxygen Meter. This sensor monitored oxygen concentration during all

experiments. During oxygen uptake experiments, all chambers were sealed. At other times the system was continuously aerated.

Algal Culture

Tahitian strain *Isochrysis galbana* was used as food. *I. galbana* is regarded as a high quality food of bivalves (Stromgren and Cary 1984). *I. galbana* had ellipsoid cells which measured 5 by 4.5 by 4.5um. *I. galbana* grew well in culture, and did not sediment within the experimental system.

Five hours before use, 20 l of log phase algal culture was left in the dark to complete cell division, then transferred to the darkened, 25 l experimental resevoir. Continuous agitation by a magnetic stirrer prevented algae from sedimenting.

Food Concentration Regulation

A perfusion pump pulled seawater from the main chamber through a Turner Designs Model 10-005 Fluorometer. The fluorometer had a stable output (<0.8V) at all food levels used. The output was amplified and passed through an analog comparator. This signal was then digitised and fed into a data logger.

A dose of algae was inoculated when the amplified fluorometer output fell below the voltage of a stable reference signal. The dose inoculation circuits switched off, then reversed a peristaltic pump for a period controlled by a variable resistor and a timer chip. The pump motor was then reset to run in the original direction.

Three one-way valves were mounted on top of the main chamber. Two valves controlled the flow of algal culture through the inoculation system. The third controlled the flow of filtered seawater into the main chamber, displacing water containing metabolites.

When the peristaltic pump ran forwards, algae was pumped through a one-way valve and around a continuous circulation loop. Continuous motion prevented algae from settling in the tubing. Suction kept a second (inoculation) valve closed while the peristaltic pump ran forwards.

When the peristaltic pump was reversed, suction closed the one-way valve on the circulation loop, and compression opened the inoculation valve. The pump injected algal culture into the main chamber until the peristaltic pump ran forwards again. The amount of algae inoculated in each dose was determined by dose duration, peristaltic pump speed and algal culture density.

After inoculation of a dose of algae, a lockout system prevented the addition of more algal culture for 30 seconds. This allowed algae to mix and register on the fluorometer before another dose could be inoculated. Inoculation of each dose of algae was recorded on either an analog chart recorder or a digital data recorder.

Physico-chemical Control

Temperature was regulated within the range 12-18^{o}C ($\pm$0.2^{o}C) within a temperature controlled room. Salinity was controlled by the addition of distilled water, and was measured daily using a YSI Model CM 30 ET Conductivity Meter. Current speed was regulated by varying the speed of the Archimedes Screw.

An air compressor provided aeration through a Pasteur pipette. The feeding of mussels appeared to be sensitive to biogenic odours occurring in the shellfish hatchery. The compressor was therefore located outside the hatchery.

Filtered seawater water was added at 1 l h^{-1} to displace water containing algal and mussel metabolites, and replaced water 1.6 times in 24 h, maintaining ammonia levels of less than 0.1 ppm. Displaced water flowed into the 25 l overflow reservoir, which was weighed daily.

Experimental Procedures

Mussels were acclimated for 3 d at 15^{o}C, and were fed *I. galbana*. While acclimating, mussels attached their byssal threads to a stiff plastic mesh. At the start of each experiment, the mesh was transferred to the perspex tube in the main chamber without disturbing the byssal threads of the experimental group of mussels.

Experiments were conducted using 30-100 mm mussels of length, and were run at 15^{o}C, 34 ppt salinity and at 10 cm s^{-1} current speed. During experiments, filtration rate was measured at 10-100 min intervals. The gape of mussels was observed twice daily, and oxygen levels were maintained above 5 ppt by controlling of the rate of aeration.

Food concentration was measured by counting *I. galbana* samples taken from the main chamber four times daily. Algal culture cell counts were made twice daily. Algal counts were made using a model Fn Coulter Counter (70um aperture, Attenuation=0.5, Aperture Current=32, Threshold= 10%). An MCV/Haematocrit device was set at a lower threshold to detect any digested food particles present in the food resource.

Data Analysis

The rate of algal inoculation required to maintain food concentration was recorded on a data log every 100 min. Alternatively, dose rates were recorded on a chart recorder. Count period, fluorescence of chamber water, and the absorbance of the algal culture used was also logged.

Filtration rate was defined as the volume of water swept clear of food particles per unit time. Filtration rate was determined by first calculating grazing rate (Equation 1). I then derived filtration rate by dividing through by the food concentration (C_c: Equation 2). Grazing rate is equivalent to ingestion rate only while pseudofaeces are not being produced (Gallager and Mann 1980).

Equation 1. $$G_r = \frac{(n * D_v * A_c) - (O_v * C_c)}{T}$$

Equation 2. $$V_f = \frac{(n * D_v * A_c)}{T * C_c} - \frac{O_v}{T}$$

where G_r=grazing rate (cells h^{-1}), V_f=volume filtered (l h^{-1}), n=number of doses of algae inoculated, D_v=dose volume (l), A_c=algal culture cell density, T=duration of dose count (h), C_c=cell density in main chamber and O_v=volume of overflow in time T.

System Evaluation

Within 5 h of transfer to the experimental system mussels filtered *I. galbana* at stable rates. *I. galbana* was ingested readily. Examination under a microscope revealed that the faeces produced from *I. galbana* were comprised of highly degraded algal cells.

Stable food concentrations of 20,000-100,000 cells ml^{-1} *I. galbana* were maintained during these experiments. Maximal hysteresis of food concentration of $\pm$7% occurred at 20,000 cells ml^{-1}. At higher food concentrations, this hysteresis declined to less than 2%. The new feeding system was therefore able to regulate low, stable food concentrations of 0.3 mgC l^{-1} *I. galbana*. In later studies, stable food concentrations of 0.03-10.8 mgC l^{-1} were maintained (Section 3.2). Thus, the new system could maintain a range of food concentrations exceeding that of 0.3-4.0 mgC l^{-1} recorded near mussel communities (Section 2.1; Hickman, Waite, Illingworth and Meredyth-Young, in prep).

Stable food concentrations below 1 mgC l^{-1} were not achieved by Winter's (1973) automated system (Navarro and Winter 1982), or another system which used photometric food concentration sensors (Riisgard and Mohlenberg 1979). However, the new system had comparable performance to the fluorometric system of Gallager and Mann (1980). Both my system and that of Gallager and Mann can facilitate investigation of filtration rates of filter feeders at low, natural concentrations of food.

The major advantage of my system over those of Riisgard and Mohlenberg (1979) and Gallager and Mann (1980) was achieved by integrating the experimental systems. Major labour costs incurred in constructing energy budgets include the culture of algae and the determination of feeding rates. Little time was needed to determine digestive efficiency and oxygen uptake. Energy budgets were therefore derived (Section 3.2) at similar costs to costs of well managed long-term feeding experiments. This integrated system can provide more comprehensive descriptions of grazer performance, without incurring an unacceptable increase in workload.

The incorporation of faecal traps improved the reliability of the integrated system. Faeces can fragment and perturb feeding experiments (Hildreth 1980). Gallager

and Mann (1980) state that degraded phytopigments did not fluoresce and disturb their system. However, degraded phytopigments do fluoresce (Section 2), and can perturb feeding experiments conducted in experimental systems which use fluorometers to regulate food concentration. Capture of faecal pellets should therefore reduce breakage of faeces and facilitate the precise regulation of food concentration.

My system also simulated a diverse range of environments. Low turbulence flows were produced over a wider range of current speed than used by Winter (1973) or Riisgard and Mohlenberg (1979). Oxygen concentration ($\pm$0.3 ppm), salinity ($\pm$0.2 ppt), and temperature ($\pm$0.2^{o}C) were also controlled. The wide range of nutritional, dynamic and physico-chemical conditions which were regulated in the new system (this section) allowed more realistic simulation of sub-littoral environments. This represents a significant improvement over all previous systems, and these attributes were used to assess the separate impacts of current speed, oxygen concentration, salinity, food deprivation and spawning on the feeding of mussels.

Current Velocity

Filtration rate was measured over a period of 12 h at four different current speeds of 5, 10, 15 and 28 cm s^{-1}. This range of velocities represented the range sampled near mariculture systems (Section 2), and reflects the maximum range in which feeding should be measured using the system described above. A single group of 6 mussels of 60mm length were fed at 0.4 mgC l^{-1} *I. galbana*, and at 15^{o}C, 34 ppt salinity and 6 ppm O_2. A randomised block design was used to reduce the possible impact of undetermined time dependent effects, and errors were determined using measurements of filtration rate made during consecutive 100 min periods (ANOVA).

Oxygen Concentration

Six mussels of 80mm length were pre-fed for 24 h at 0.7 mgC l^{-1} *I. galbana*. During the experiment, mussels were allowed to feed at 0.7 mg l^{-1} food at 15^{o}C, 34 ppt salinity and in currents of 10 cm s^{-1}. Filtration rate of this single group of mussels was measured as oxygen concentration declined from 5.0 ppm O_2 (0800 hours, Day 1) to 1.5 ppm O_2 overnight, then increased again to 4.6 ppm O_2 (1320 hours, Day 2). Oxygen concentration was monitored using a YSI Model 57 Oxygen Meter. Filtration rates were determined 3 times within each consecutive 45 min period. These three measurements were used to estimate errors in determining feeding rate during each 45 min period. The statistical significance of results was tested using ANOVA when the groups of observations being compared had similar variance; otherwise the Kruskal-Wallis Test was used to determine the significance of results.

Salinity

Four mussels of 90mm length were acclimated at 34 ppt salinity, and fed at 1.8 mgC l^{-1} *I. galbana* at 15°C. Filtration rate was measured at 6ppm O_2 and in flows of 10 cm s^{-1} for 5 h. Distilled water was then added to reduce salinity to 25 ppt. This change in salinity occurred within 3 minutes. Filtration rate was then measured at 25 ppt salinity for 15 h. During this period oxygen tension did not vary significantly. Results are presented as a simple time series derived from consecutive observations made 15 minutes apart.

Food Deprivation

The two following experiments determined how prior starvation affected the feeding behaviour of mussels. Both experiments were conducted at 15°C, 34 ppt salinity, 10 cm s^{-1} current speed, and at 6 ppt O_2.

Six mussels of 80mm length were pre-fed 0.3 mgC l^{-1} *I. galbana* for 5 d, then starved for 24 h. After starvation, mussels were fed at the low concentration of 0.3 mgC l^{-1} food for 72 h. Filtration rate was determined every 100 min both before mussels were starved, and for 44h after food supplies were restored. The mean and variance of filtration rate was estimated for 3 adjacent 100 minute time intervals.

In a subsequent experiment, four mussels of 90mm length were pre-fed 1.8 mgC l^{-1} *I. galbana* for 24 h, then starved for 24 h. Mussels were then fed again at 1.8 mgC l^{-1} *I. galbana.* Filtration rate was determined at 15 min intervals for 28 h after food supplies were restored. Filtration rates are presented as the simple time series which was later analysed using spectral analysis (BMDP1T).

Male Spawning

The remaining studies which are described below were all conducted at 15°C, 34ppt salinity, 10 cm s^{-1} current speed and between 5 and 6ppm oxygen tension.

Six mussels (4 male, 2 female) were exposed for 96h to a food concentration of 0.4 mgC l^{-1} *I. galbana,* and over this period of 96h their rate of filtration was determined. The four male mussels spawned after 48h had elapsed. After spawning, both algae and sperm cells were counted using the Coulter Counter. Sperm cells were counted as the number of sperm plus algal cells counted at a 5% threshold setting, minus the number of algae counted at a 10% threshold setting. The sperm remaining 17 h after males had spawned were flushed from the system with filtered water at 15°C.

Filtration rates were measured on this single group of mussels, and 95% confidence intervals were determined by ANOVA using consecutive measurements of feeding made at intervals of 20 min. Filtration rates were measured until filtration had recovered to the rate recorded before spawning had occurred.

Female Spawning

A single female spawned in 4 l filtered seawater. Eggs were left in seawater for 20 h. This water was then refiltered through Whatman GF/A paper. Spawn water and eggs were stored separately for 30 and 210 min, respectively, before being inoculated into a chamber containing actively feeding mussels.

Six unspawned mussels (3 male, 3 female) were fed at 0.3 mg l^{-1} *I. galbana.* After 48 h, 2 l filtered spawn water was added to the main chamber, and 3 h later the eggs were also inoculated. Filtration rates were recorded for 48 h before and then 20 h after spawn water was added. The 95% confidence intervals were determined by ANOVA using 3 measurements of feeding rates made 20 min apart.

RESULTS

Current Velocity

Mussels filtered at rates of 3.4, 3.3, 3.3 and 3.4 l h^{-1} at flows of 5, 10, 15 and 28 cm s^{-1}, respectively. Filtration rate did not therefore change significantly with current speed within the range of 5-28 cm s^{-1} (ANOVA, F=0.78, df=3, p=0.51, Fig 2), a range similar to that recorded outside of mussel farms in Marlborough (Section 2.1).

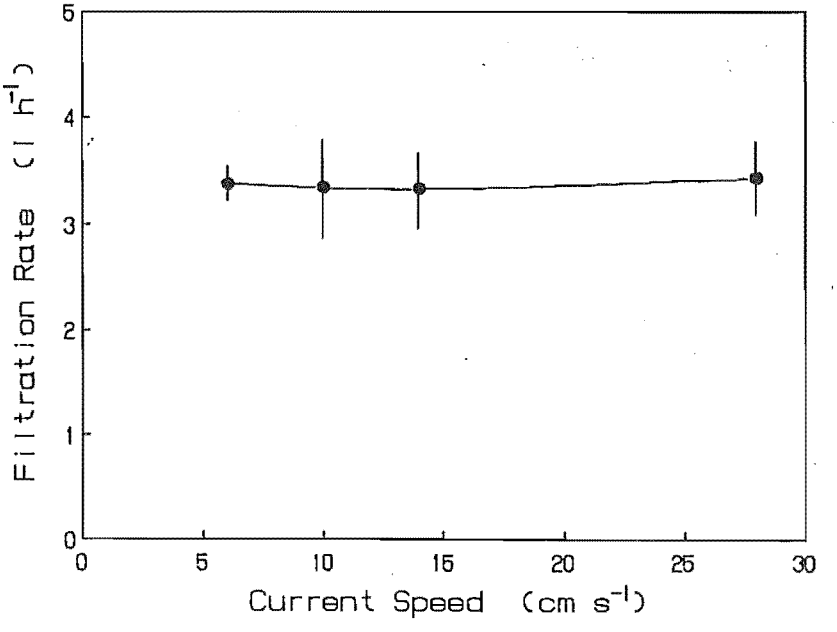

Figure 2. Effects of current velocity on filtration rate in 60mm length class mussels. Vertical bars represent 95% CI.

Oxygen Concentration

At the start of the experiment, mussels filtered 4.0 l h^{-1} at an oxygen concentration of 5.0 ppm O_2 (Fig 3). Filtration then declined to 2.71 l h^{-1} at 3.5 ppm O_2 (ANOVA, F=45.8, df=1, p=0.006). Below 3.5 ppm O_2, plotted confidence intervals indicated that filtration rate decreased consistently to only 0.4 l h^{-1} at 1.5 ppm O_2. This was one tenth of the rate recorded at 5 ppm O_2. Filtration did not increase markedly during the 12 h mussels fed at 1.5 ppm O_2, suggesting rapid acclimation to this unusually low oxygen level did not occur. After aeration was restored, more rapid filtration occurred than was recorded at similar oxygen concentrations while oxygen concentration was declining. However, the cause of minor fluctuations in filtration as oxygen concentrations changed was not determined. Whereas filtration rates increased markedly with oxygen concentration from 0.4 l h^{-1} at 1.5 ppm O_2, to a maximum of 4.2 l h^{-1} above a threshold of 3.4 ppm O_2 (Kruskal-Wallis Test, p<0.001), similar feeding rates occurred at both the beginning and end of this experiment.

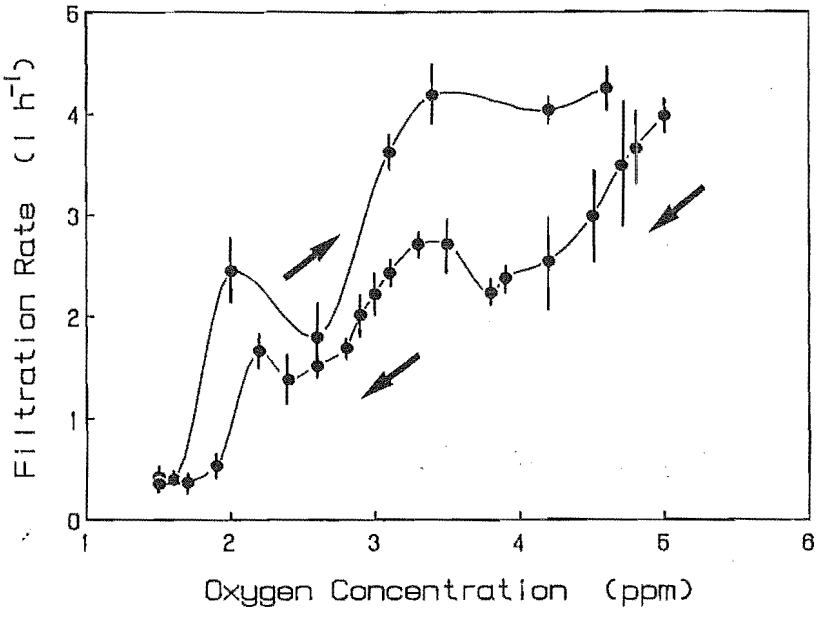

Figure 3. Effects of oxygen concentration on filtration rate. Arrows indicate the order of observations. Vertical bars represent 95% CI.

Salinity Shock

Mussels filtered at 5.3 l h^{-1} for 5 h before salinity was reduced (Fig 4). After salinity was reduced from 34 to 25 ppt, no filtratory activity was recorded for four hours. During this time, mussels gaped intermittently and probably inhaled water. After 4 h, mussels extended their opening period and filtered algae from the water. Filtration rate increased progressively to 5.9 l h^{-1}, 8.5 h after the salinity shock. Filtration rate stabilised at 5.3 l h^{-1} at 25 ppt. This rate was not different from the rates recorded before the salinity shock occurred (ANOVA, F=0.005, df=1, p=0.94).

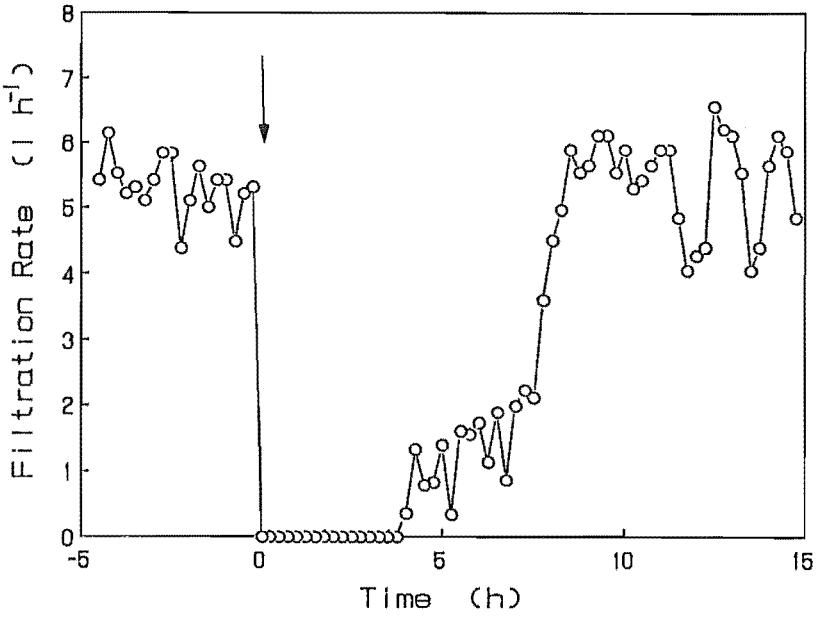

Figure 4. Effects of a salinity shock on filtration rate. The arrow indicates when salinity decreased from 34 to 25 ppt.

Food Deprivation

At 0.3 mgC l^{-1} *I. galbana*, filtration rate increased from 3.4 l h^{-1} before starvation to 4.5 l h^{-1} after starvation, an increase of 32% (ANOVA, F=730.5, df=1, p=0.0001, Fig 5). Filtration rate peaked briefly at 5.1 l h^{-1} two hours after food supply was restored, then oscillated slowly during the next 18 h before stabilising at a rate of 4.5 l h^{-1} thirty hours after food supplies to mussels were restored.

At 1.8 mgC l^{-1} food, mussels filtered 0.3 l h^{-1}, 15 min after food supply was restored (Fig 6). Mussels had responded to the restoration of food supply within 20 min, and consistently increased filtration rate to a maximum of 9.9 l h^{-1} 1.5 h later. Two hours later, filtration rate fell to 2.2 l h^{-1} and remained low for 2.5 h, before increasing to 3.8 l h^{-1}. Filtration continued at this rate for 2 h before decreasing briefly and increasing to 5.6 l h^{-1} for 3.2 h. Filtration rate then declined to a low of 2.0 l h^{-1} and remained depressed for 2.2 h before stabilising at 4.8 l h^{-1}. This stable filtration rate was only 48% of maximum observed filtration rates (ANOVA, F=1082, df=1, p<0.0001).

Spectral analysis (BMDP1T) showed cyclic changes in filtration occurred over 2.5-5 h. Feeding behaviour therefore responded to changes in ration within 1.2-2.5 h. It was later determined that the mussel had a gut passage time of 2.5 h at 15°C (Section 3.2.2). This gut passage time exceeded the 1.2-2.5 h lag recorded between the ingestion of food and the subsequent modification of filtration rate by the mussel. At high food concentrations, my results therefore suggested that delayed negative feedback from gut fullness sensors may have affected rates at which mussels filtered food from seawater.

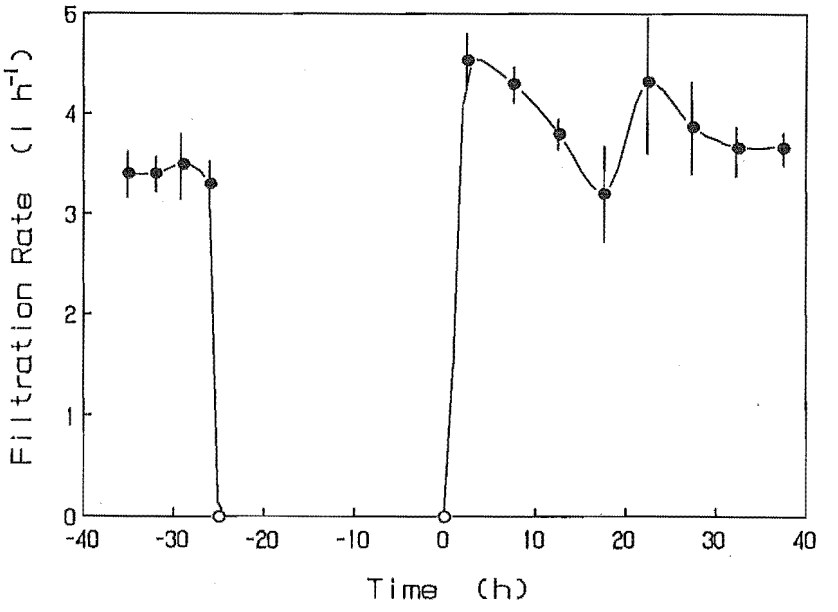

Figure 5. Effects of starvation on filtration rate at unusually low food concentrations (0.3 mgC l^{-1}). Food supply ceased at t=-24 hours and was then restored at t=0 hours (see arrows).

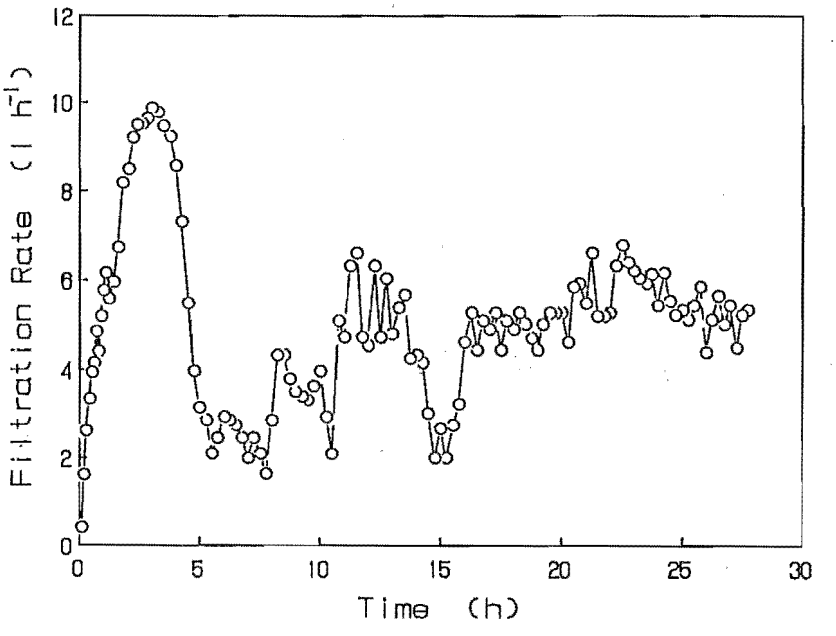

Figure 6. Effects of starvation on filtration rate at high food levels. Food supply was restored at t=0 hours.

Effects of Male Spawning

Before discharge of sperm was first observed mussels filtered at a mean rate of 4.5 l h^{-1} (Fig 7). One hour after spawning occurred, sperm concentrations exceeded $2x10^6$ cells ml^{-1}. At this time, filtration rate had fallen to 1.2 l h^{-1}, representing a decline of 73%. Feeding then ceased 7 hours after the spawning event occurred and this indicated that the female mussels which did not spawn had also stopped feeding in the presence of dense suspension of sperm cells.

After sperm were flushed from the feeding chamber, filtration rate increased to

3.2 l h^{-1} over 30 minutes. A light sperm discharge (97,000 cells ml^{-1}) then coincided with moderately reduced filtration rates of 2.6 l h^{-1}.

Filtration rates then increased above those recorded before sperm were extruded, and oscillated for a period exceeding 12 h. These fluctuating filtration rates may be, in part, a response to the preceding 18 h of reduced food intake rather than a consequence of spawning. Twenty hours after sperm was cleared from the main chamber, filtration rates were both stable and similar to those recorded before spawning had occurred.

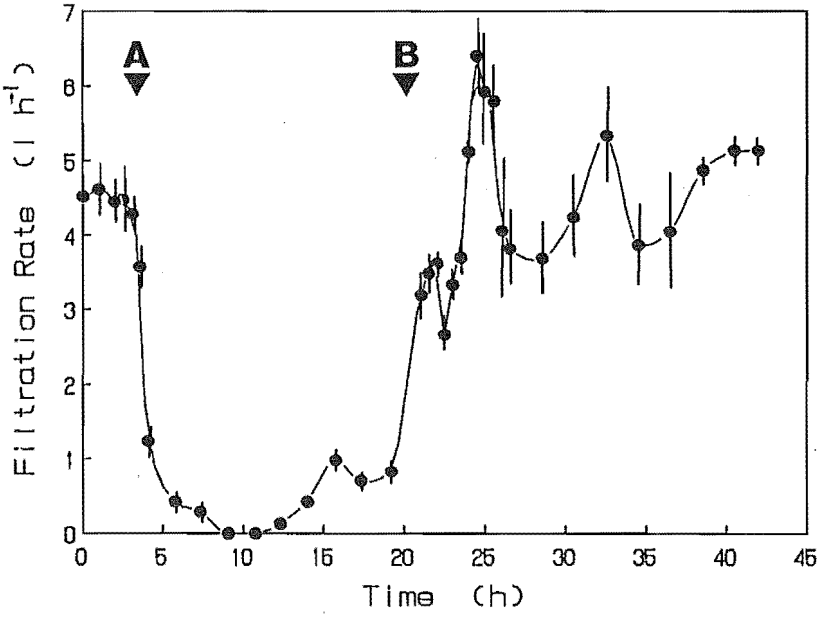

Figure 7. Effects of a male spawning event on filtration rates within a group comprised of both sexes. A: spawning observed, B: system flushed with seawater (see text). Vertical bars represent 95% CI.

Effects of Spawning by a Single Female

Prior to inoculation of spawn products mussels filtered at a rate of 4.2 l h^{-1}. After filtered water in which a female had spawned was added this filtration rate decreased by 32% for less than 60 minutes (Kruskall-Wallis Test, $p=0.05$, Fig 8). The eggs shed by the female were then inoculated, after which filtration rates decreased to 1.7 l h^{-1} over the next 30 minutes. These unspawned mussels eventually filtered at only 19% of their original rate (ANOVA, $F=56$, $df=1$, $p=0.01$), and maintained low rates for the period of 7 h after eggs had been inoculated.

Eight hours after the eggs were inoculated, mussels filtered at similar rates to rates recorded before the inoculation of spawn water. The experiment was terminated 14 h after eggs were inoculated, and at that time no eggs were found in suspension.

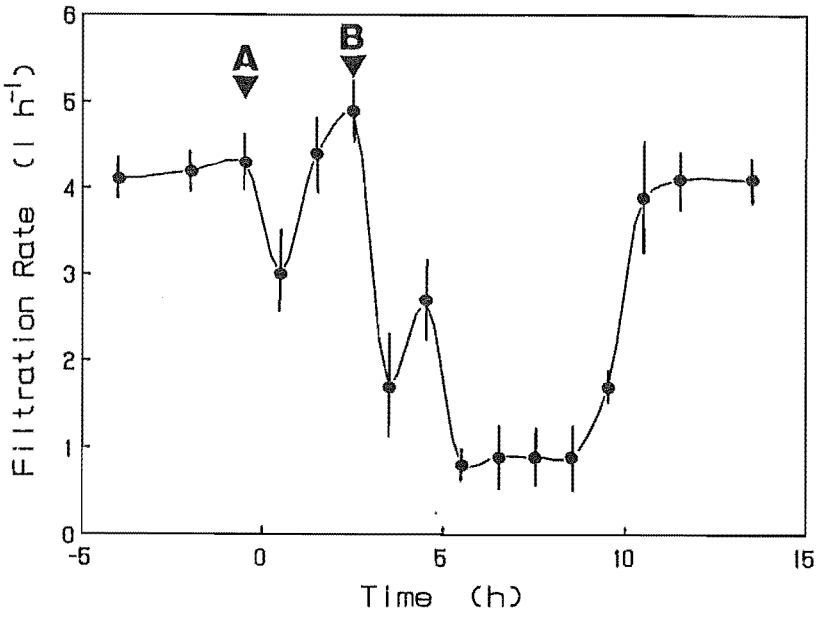

Figure 8. Effects of female spawn products on filtration rates within a group of unspawned mussels. A: spawn water inoculated, B: eggs inoculated (see text). Vertical bars represent 95% CI.

DISCUSSION

These studies were conducted to determine which factors affect food intake by *P. canaliculus* in laboratory situations. This study has shown that many factors affect filtration rates determined within a closed experimental system, and therefore probably influence energy uptake by mussels. Adequate knowledge of the effects of such factors is required to evaluate and interpret the significance of the feeding patterns recorded within various laboratory systems.

Current Velocity

Filtration rate was not affected by current speeds of 5-28 cm s^{-1}. This suggested that estimates of filtration rate, ingestion and energy uptake are not directly dependent on current speed over the above range.

In *Mytilus edulis*, filtration rate was not affected by currents of 0.5-5 cm s^{-1} (Riisgard and Mohlenberg 1979), and the apparent dependence of filtration rate on flow velocity in *M. edulis* recorded by Walne (1972) may actually result from food depletion occurring within his experimental chambers (Hildreth and Crisp 1976). However, the rate of capture of food by other filter feeders does decline above current speeds of 6.4 cm s^{-1} in crinoids (Leonard et al. 1988) and also declines from current speeds of 2 to 10 cm s^{-1} in bryozoans (Okamura 1987). Flow velocity therefore may limit food uptake by other grazers.

While filtration was not measured, Kirby-Smith (1972) stated that growth of the scallop *Argopectens irradians* was limited by food depletion at slow current speeds (0.2 cm s^{-1}), and was directly limited by flow at current speeds exceeding 12 cm s^{-1}. Wildish and co-workers (Wildish et al. 1987; Wildish and Kristmanson 1988) later showed that the feeding and growth of *Placopecten magellanicus* also declined above a similar critical flow rate of 10-20 cm s^{-1}. In *P. canaliculus*, however, filtration was not inhibited by flow velocities as high as 28 cm s^{-1}, suggesting that *P. canaliculus* was more tolerant to high current speeds than these scallops. This ability to feed rapidly in dynamic water masses may adapt mussels to life in turbulent littoral and sub-littoral environments.

Oxygen Concentration

Filtration rates of *P. canaliculus* decreased markedly as oxygen concentrations fell from 5.0 to 1.5 ppm O_2. While oxygen concentration was rising, however, maximal filtration rates occurred when oxygen concentrations increased above 3 ppm O_2. Similar thresholds have been reported for *M. edulis* (Bayne 1975), and are also recorded at concentrations of 3 ppm O_2 in *Daphnia pulex* (Cladocera: Heisey and Porter 1977).

It was notable that while oxygen concentration was increasing, filtration by *P. canaliculus* was always more rapid than rates recorded at corresponding oxygen levels while oxygen was decreasing. This suggests that partial adaptation to reduced oxygen concentration may have occurred during this study. However, these observations were made on a single group of mussels, and the causes of less consistent fluctuations in feeding rates were not determined.

Oxygen concentrations recorded in densely populated mussel farm communities seldom fell below 5 ppm O_2. However, less than 2 ppm oxygen tension was found within poorly aerated laboratory systems. Thus, the detrimental effects of reduced oxygen tension recorded above may be largely confined to other natural habitats, and to experimental systems that have inadequate aeration.

Salinity

The impact of changes in salinity on feeding by mussels had been determined only for *M. edulis* where filtration declined markedly on exposure to salinities below 20 ppt (Widdows 1985). At higher salinities *M. edulis* adapted well to changes in salinity. In *P. canaliculus*, rapid feeding occurred 8 h after salinity had been reduced from 34 ppt to 25 ppt. In an unreported trial, however, *P. canaliculus* ceased to gape and feed for 24 h after immersion in water of 17 ppt salinity. Thus, while moderate variations in salinity affected feeding by both mussels temporarily, severe salinity shocks interrupted the feeding of both mussels for protracted periods. It is therefore possible that *P. canaliculus* and *M. edulis* can tolerate similar ranges of salinity.

P. canaliculus appeared to adapt to reduced salinity and started to feed 4 hours after a substantial salinity shock. This period is similar to the 3 h taken by *M. edulis* to mobilise amino acids for cell volume regulation after a salinity shock (Pipe and Moore 1985). After the salinity shock, filtration by *P. canaliculus* declined for 8 hours, whereas *M. edulis* took 10 h to show marked osmotic adaptation to 40% decreases in salinity (Gilles, 1982) and took 7-10 days to acclimatise to major changes in salinity (Thede 1963). These correspondences may be coincidental, but it could be interesting to determine whether *P. canaliculus* may have commenced feeding before the mussel had fully adapted to it's new salinity regime.

Optimal growth of other mussels occurred in salinity ranges of 27-65 ppt (*M. viridis*: Sivalingham 1977) and 20-35 ppt (*M. edulis* spat: Hrs-Brenko and Calabrese 1969), but at only 12-17 ppt in spat of the oyster *Crassostrea virginica* (Chantry et al 1985). Although my laboratory studies only provided short-term measures of response to salinity, *P. canaliculus* did adapt rapidly to feed at 25-34 ppt salinity in the laboratory. Again, this range is similar to that defined for the three species of bivalves listed above.

Food Deprivation

Conflicting descriptions of interactions between food concentration and filtration rate have emerged from different studies of feeding in *M. edulis*. In studies during which filtration was determined within 3 h of disturbance, filtration rate did not vary markedly with food concentration (Thompson and Bayne 1974; Widdows 1978a). In experiments where filtration was monitored for 3-24 hours after disturbance, filtration decreased markedly at high food concentrations (Winter 1973; Riisgard and Randlov 1981; Sprung 1984a).

The two most recent of the above studies have shown that *M. edulis* only commences regulating filtration rate 3-12 hours after experiments begin (Riisgard and Randlov 1981; Sprung 1984a). Filtration by *P. canaliculus* also varied substantially over time. When *P. canaliculus* fed at low food concentrations, prior starvation enhanced filtration rates by 32% for 10 hours. At high food levels, previously starved mussels initially filtered at double their final rate for over two hours. During that period, mussels ingested twice the ration ingested after filtration had stabilised at lower, stable rates. These initial, elevated feeding rates were most pronounced during the first few hours after food deprivation, but persisted for over 10 hours after starvation. Thus, experimental studies on *P. canaliculus* could overestimate food intake if mussels are not allowed adequate time to adapt to a new experimental situation.

After filtratory regulation had become established, *P. canaliculus* both filtered less water and ingested less food than occurred soon after the mussel's food supply was restored. Food deprivation also enhanced feeding rates of *M. edulis* (above), *Daphnia*

magna (Cladocera: Ringelberg and Royackers 1985) and *Temora longicornis* (Copepoda: Morales 1987) for several hours before filtration declined to low, stable rates. These animals may therefore show similar gross responses to food deprivation.

Other animals regulate their feeding rates through feedback from gut fullness sensors (Windell 1976; Stemberger 1986) and the hypothesis that gut fullness affects the feeding behaviour of this mussel was therefore tested. On exposure to high food concentrations after being deprived of food for 24 hours, *P. canaliculus* alternated between rapid and slow filtration rates every 0.5-1.0 gut passage times. The concurrence of my estimates of feeding periodicity and gut passage time provided the first indication that delayed feedback from digestive tract receptors could regulate filtration by *P. canaliculus* fed at high food concentrations. This delay between the ingestion of food and onset of a regulated feeding behaviour indicates that carefully managed, long-term experiments should provide more dependable measures of feeding rates than do short feeding experiments.

Feeding Behaviour After Spawning

The presence of sperm of *P. canaliculus* strongly inhibited feeding by the mussel. Reduced feeding rates could be caused in three ways. Males may decrease filtration rate after spawning to limit the ingestion of sperm, compatible eggs and progeny. But unspawned females also ceased to feed without attaining an obvious selective advantage. Recovery of filtration rate after flushing sperm cells from the system indicated that feeding was not inhibited by intrinsic agents, and that behavioural limitation of feeding was either a short-term event, or did not occur. Secondly, chemicals secreted by, or discharged with sperm may inhibit feeding, but while this remains possible no chemical suppression of feeding was evident after sperm were cleared by mussels which fed after a minor spawning event. Thirdly, presence of sperm cells may inhibit feeding by mussels of both sexes. This theory best fits the available data as filtration rates recovered rapidly after sperm was either deliberately removed or eaten by mussels.

The filtration rate of *P. canaliculus* was also sensitive to both the concentration of sperm present and the period that mussels were exposed to sperm. While mussels stopped feeding at high sperm concentrations ($2x10^6$ cells ml^{-1}), feeding activity resumed after sperm were removed. In contrast, *M. edulis* showed no decline in feeding activity in the presence of 15-103,000 sperm ml^{-1} (Newell and Thompson 1984). While strong intrinsic, post-ejeculatory suppression of feeding occurred in *M. edulis* for ten days after spawning (Newell and Thompson 1984), *P. canaliculus* showed no intrinsic suppression of feeding rates. Thus, different mechanisms regulated feeding behaviour after males of each species had spawned.

When unspawned mussels of both sexes were then exposed to eggs produced by a

single, different female, their filtration also declined markedly. This is the first demonstration that the presence of suspended eggs can inhibit filtration by mussels. Eggs of *P. canaliculus* inhibited feeding three times more strongly, and for fourteen times longer than any effect of dissolved chemical agents. This indicated that the observed inhibitory effect was due primarily to the presence of eggs. The accumulation of eggs near a mussel colony may therefore limit food uptake by that community.

These studies, therefore, demonstrated that feeding by mussels was inhibited in the presence of both male and female gametes. The reduction in food intake resulting from the presence of gametes probably reduced both the energy uptake and growth of *P. canaliculus*. Also, entrapment of gametes during feeding of parental mussel communities may limit reproductive efficiency. While some captured eggs were ejected in pseudofaeces by *M. edulis* (Newell and Thompson 1984), capture of gametes could result in the ingestion of gametes, damage to gametes or isolation of gametes from compatible gametes by barriers of pseudofaecal mucus. It is therefore suggested that mussels that feed after spawning can reduce the number of gametes capable of producing fertilised eggs. In field populations of *P. canaliculus*, spawning events involved most adult mussels in the community (Meredyth-Young, Pers Comm). During these mass spawning events, reduction of filtration could also limit ingestion of both gametes and embryos, maximise cohort survival, and enhance the reproductive viability of mussel communities. Mechanisms which reduce feeding after spawning events can therefore confer selective advantage.

In benthic communities, the intensity with which feeding is inhibited after spawning may be attenuated by sedimentary and transport processes which remove gametes from the community. *P. canaliculus* only limited it's feeding in the presence of gametes, and so feeding of littoral communities may decline only when spawning occurs in currents which are too slow to transport gametes away from the parental mussel community. Such conditions may occur most often in environments typified by low tidal currents and reduced wave activity. In many situations, gametes may be transported away from littoral colonies soon after extrusion, and before the presence of gametes inhibits feeding for protracted periods. However, deepwater communities of mussels live within boundary layers that retard the movement of water (Frechette and Bourget 1985a) and delay the removal of spawn products. Extruded gametes could remain near these mussels, and inhibit feeding by *P. canaliculus* for protracted periods.

Enhanced reproductive success may be attained at a cost of reduced parental assimilation. This study indicated that *P. canaliculus* would only reduce feeding rate while marked concentrations of gametes were present. This feeding behaviour would enhance survival of gametes and embryos at a low energy cost to breeding mussels. In contrast, *M. edulis* reduced feeding rate for ten days after spawning, even though no

gametes were present (Newell and Thompson 1984). If *P. canaliculus* had markedly reduced feeding rates for ten days then the decline in energy uptake may reduce the energy available for growth and reproduction by over 40% (data from Section 3.3.1). *M. edulis* may therefore enhance the survival of it's progeny at higher cost to adult mussels than did *P. canaliculus*. Interesting variations therefore occur in the cost-benefit ratios of the different nutritive strategies exhibited by sexually active communities of mussels of two different species.

Synopsis

Collectively, my studies indicate that feeding by *P. canaliculus* is determined by interactions occurring between a number of different intrinsic and extrinsic factors. Thus, supposed minor controls of feeding should be carefully evaluated before nutrient budgets are compiled. In particular, the feeding history of the mussel and the stability of food concentration may affect the behaviour of bivalves feeding within laboratory systems. Thus, the development of more sophisticated experimental feeding systems (Gallager and Mann 1980; this study) can be justified by (1) an enhanced ability to simulate natural environments, and (2) improved consistency and reliability of results.

SECTION 3.2.1.

Effect of mussel size and food concentration on feeding in Perna canaliculus fed a high quality food

ABSTRACT

In 3 size classes of mussels (30, 60 and 80mm length) maintained at 15°C, five different types of feeding behaviour occurred as food concentration was increased.
1. Filtration rate increased from 0.03 mgC l^{-1} food to a maxima at 0.3 mgC l^{-1}.
2. Filtration rate then declined by 30% as food concentration increased to 0.6 mgC l^{-1}.
3. Uniform filtration occurred between 0.6 and 1.0 mgC l^{-1}. 4. From 1.0-4.1 mgC l^{-1}, filtration declined and a maximal ration was ingested. 5. Above 4.1 mgC l^{-1} food, mussels filtered at minimal rate, appeared to ingest a maximal ration, and rejected excess food in pseudofaeces.

The mussels maximal ration was proportional to shell length raised to the power 3.01. The 30mm length class ate a larger fraction of it's maximum ration below 1.0 mgC l^{-1} food than did larger mussels, and it's maximum ration also contained 28% more food per unit body mass than the maximum ration of the 80mm length class.

Below 1.0 mgC l^{-1} food, ingestion rate was the primary determinant of energy uptake. Neither food concentration nor ingestion rate affected assimilation efficiency. The oxygen uptake of mussels doubled as the volume of food they ingested increased.

Growth was maximal in mussels consuming their maximal ration. On maximal ration, the 30mm class had a maximal gross growth efficiency of 0.48 compared with 0.66 in the 80mm class. Maximal growth potential varied little (3.7-4.0% body mass d^{-1}) between length classes. Below 1 mgC l^{-1} food, reduced food availability induced a marked decline in "Scope for Growth".

INTRODUCTION

Prior to my study there was no information on the dynamics of food uptake by *P. canaliculus*, but studies had been made using other bivalves. Low food concentration has been shown to limit the feeding and growth of mussels (eg Thompson and Bayne 1974; Navarro and Winter 1982; Stromgren and Cary 1984). Low food concentration also affects gametogenesis (Blake and Sastry 1978; Chanley 1981), and production of faeces (Navarro and Winter 1982) and pseudofaeces (Gerdes 1983). Thus, reduced food supplies

can limit the mussel's vitality (Sindermann 1977) and rates of transfer of carbon within an ecosystem (Dame et al. 1980; Kaspar et al. 1985).

The role of high food concentration is, however, less clear. While high food concentration has been shown to promote regulated, rapid food intake, energy uptake and growth in *M. edulis* (Winter 1973; Riisgard and Randlov 1981; Sprung 1984a,b,c; Stromgren and Cary 1984), other studies indicated that reduced growth (Thompson and Bayne 1984) or growth efficiency (Widdows 1978a) occurs at high food levels. The present study measured feeding rates and energy budgets of *P. canaliculus* in an attempt to determine how this mussel may respond to different concentrations of food.

Many authors have shown that the filtration rates of mussels increase markedly with mussel size (see Winter 1978a,b; Sprung 1984b). However, both mussel length and food concentration may interact in a complex manner to determine feeding and growth (eg Thompson and Bayne 1974; Navarro and Winter 1982; Sprung 1984a,b). Thus, it is necessary to measure filtration and "Scope for Growth" in response to variation in both food concentration and mussel size.

Experiments of short duration have recorded unusually high filtration rates for *P. canaliculus* (Section 3.1). Rapid filtration may occur due to inadequate acclimation of mussels to the feeding regime prior to experiments (Riisgard and Randlov 1981; Sprung 1984b; Section 3.1). I therefore determined the energy budgets of three size classes of *P. canaliculus* using measurements made during a period of 24 hours. An automated feeding system (Section 3.1) was used to determine energy flow through *P. canaliculus* over a two hundred-fold range of food concentration. The hypothesis tested was that *P. canaliculus* fed efficiently and had high, positive growth potential at high concentrations of food.

MATERIALS AND METHODS

Experimental Design

Mussels of 30, 60 and 80mm length classes were collected from longline in Mahanga Bay, Wellington Harbour (41^{o} 19'S, 174^{o} 51'E). Each size class was comprised by groups of 44, 10 and 6 mussels, respectively, which had dry tissue weights of 0.11g, 1.32g and 3.73g and condition indices ([dry tissue weight*100]/total drained weight) of 5.5%, 8.8% and 10.1%. Each group of mussels contained mussels of similar length ($\pm$2mm) at condition indices sampled in Mahanga Bay. The above differences in condition therefore reflect, in part, the maturation of mussels as they grew. Each group (size class) of mussels was acclimated for 5 d at 15^{o}C, and while maintained at 34 ppt salinity and fed at 0.5 mgC l^{-1} of the food species *Isochrysis galbana* (Tahitian strain).

The automated system described in Section 3.1 was used to measure filtration and ingestion rates, assimilation and oxygen uptake. Feeding rates and energy flow were recorded at nine to twelve food concentrations of between 0.03 and 10.8 mgC l^{-1}. Each size class of mussels was fed at each food concentration for 22h, and at each food level the filtration and ingestion rates, assimilation efficiency and oxygen uptake of each length class was determined. Feeding was determined continuously, but only those observations made overnight and after feeding rates had stabilised were used to calculate mean feeding rates and 95% confidence intervals. Thus, feeding rates were measured during 18 to 22 consecutive periods of 40 min. Carbon uptake from food was estimated using faeces produced during the 22h feeding period. Oxygen uptake was determined at the end of each feeding period. The methods used to determine feeding rates are described in Section 3.1. Other methods are detailed below.

Because non-randomised experiment designs can induce time dependent changes in experiments (Snedecor and Cochran 1980), food concentration was alternately increased and decreased in successive experiments to detect possible time dependent artifacts. Such artifacts were not found. Food concentration was increased by factors of 1.6 daily, or decreased by factors of 0.62 daily during alternate studies on mussels of different length. At the end of each experiment, filtration was also measured at one food concentration used during the experiment. Similar filtration rates were recorded both during, and at the end of experiments.

After each experiment, maximum shell length of each mussel was measured, and variation in length was determined by ANOVA. Total drained weight and dry tissue weight (24h at 100^{O}C) were recorded and used to determine the condition index of mussels ([dry weight*100|/total drained weight). Dry aliquots of mussel tissue were then ground, pelleted, and bombed in a Parr Microbomb Calorimeter.

Algal Suspensions

Mussels were fed *I. galbana* grown in semi-continuous batch culture. Algal culture densities were measured at the start and end of studies at each food concentration by diluting them 1:10 and making four cell counts with a Model Fn Coulter Counter; all counts were corrected for coincidence. Aliquots of counted culture (100ml) were assayed for dry weight, and ash free dry weight and particulate organic matter (mg l^{-1}: see Strickland and Parsons 1968). Cell carbon was determined as the ash-free dry weight contained in 100ml aliquots of culture, divided by the number of algal cells present in an aliquot from the same sample of culture.

The food concentration present in the vicinity of experimental mussels was also determined from samples that were collected from the feeding chamber four times each day, and in water collected from the overflow resevoir each morning.

Feeding Rates and Energy Balance

Ingestion rate was determined from quantities of algae inoculated to maintain algal concentration, and filtration rate was derived by dividing this by the concentration of food (Section 3.1). Mussels were positioned to reduce filtering of exhalant water; <1% of grazed water was refiltered. Experiments were conducted at $15^{o}C$, 34 ppt salinity, and at 10 cm s^{-1} flow.

Assimilation efficiency (AE) was measured according to Conover (1966), and corrected for loss of inorganic tracers (Bjorndal 1985). Bjorndal advocates the use of the total carbon collection method (see Dagg 1976) to determine a factor correcting for losses of Particulate Inorganic Matter (eg. salts) that occur within the digestive tract, and which cause over-estimation of AE when using Conover's method. Faeces sedimented after 22 h feeding were all collected in a pipette, gently washed, then frozen at $-18^{o}C$. Faeces were later thawed, dried, weighed, ashed and reweighed to determine their carbon and inorganic content.

The oxygen uptake by mussels, and in apparatus with mussels excluded (control), was measured after mussels had acclimated for 22 h at each food concentration. A YSI Model 57 Oxygen Meter was used to measure oxygen concentration.

Somatic growth (P) plus production of gametes (G) were calculated using measurements of ingestion rate (C), egestion (F) and respiration (R), expressed in kJ. The following constants were determined experimentally, and used to solve equation 1 (below): mussel tissue contained 20.2 $\pm$0.6 kJ g^{-1}AFDW, and each cell of *I. galbana* weighed 19.3 $\pm$2.0pg. *I. galbana* was assumed to have an energy equivalent of 20.1 kJ g^{-1}DW (Romberger and Epifanio 1981). Respiration energy was calculated assuming 1 ml O_2 was equivalent to 20.1 kJ energy (Crisp 1984), and that anaerobiosis was insignificant. Excretion (U) accounted for 0.6-3.1% of absorbed energy in bivalves (Navarro and Winter 1982; Shumway and Newell 1984) and was assumed to equal zero in my calculations. Production was estimated by difference using equation 1 (Crisp 1984).

$$C = P+R+G+F+U \qquad (1)$$

However, oxygen uptake will be related to body mass. Therefore, mussels of high condition should have greater respiration losses and reduced energy for growth. GP was recalculated to compensate for variation in condition between different length classes of mussels (see Table 3, p.94). Calculations assumed that energy uptake from food was independent of the condition of mussels, and that respiration was directly proportional to body mass. To recalculate GP, respiration losses recorded during each experiment (R) were adjusted for mussels of known condition (CI_d: 5.5, 8.8 and 10.1% in mussels of 30, 60 and 80mm length, respectively) using Equation 2 (below), and resultant standardised

estimates of respiration losses (R_c) at arbitrarily defined standard condition indices of 8, 10 and 12% (CI_s) were then substituted into Equation 1 (above).

$$R_c = R*(CI_s/CI_d) \qquad (2)$$

Growth Potential ("Scope for Growth": Thompson and Bayne 1974) was defined as the energy available for somatic growth plus gamete production per unit body mass, and expressed as percentages of body energy available for growth each day. Gross Growth Efficiency [GGE = (P+G)/C] and Net Growth Efficiency [NGE = (P+G)/(C-F)] were defined according to Duncan and Klekowski (1975).

RESULTS

Feeding Rate

Five levels of food concentration were identified over which changes in feeding behaviour occurred in all 3 size classes of mussels (Fig 1). The ranges of food concentrations over which each type of feeding occurred were not markedly dissimilar in each of the size classes studied, and the pattern of feeding occurring over each level of food concentration is summarised below.

Food Conc (mg l^{-1}):	0.03-0.35	0.3-0.6	0.4-1.4	1.1-4.4	>4
Filtration Rate	Ascending	Falling	Stable	Falling	Minimal
Ingestion Rate	Ascending	Ascending	Ascending	Maximal	Maximal
Energy Uptake	Ascending	Ascending	Ascending	Maximal	Maximal
Feeding Behaviour:	Type 1	Type 2	Type 3	Type 4	Type 5

Extensive transition zones may not occur between adjacent feeding behaviours in mussels of any single length class. However, whereas moderate overlap did occur between the food concentrations over which types 2 and 3 of feeding occurred in mussels of different length, two attempts to prove that a single mode of feeding behaviour occurred between 0.3 and 4.4 mgC l^{-1} reinforced the concept of the five phase feeding model presented. In all cases, when filtration was measured within the range 0.4-1.4 mgC l^{-1} at the end of studies on each size class, the 95% confidence intervals of these points included the straight line interpolation between points plotted in Figure 1. Thus, both error bars presented in Figure 1 and verification tests indicated that a simpler feeding curve comprised of only three types of feeding behaviour could not be fitted to my data. In addition, whereas ingestion rate increased markedly with food

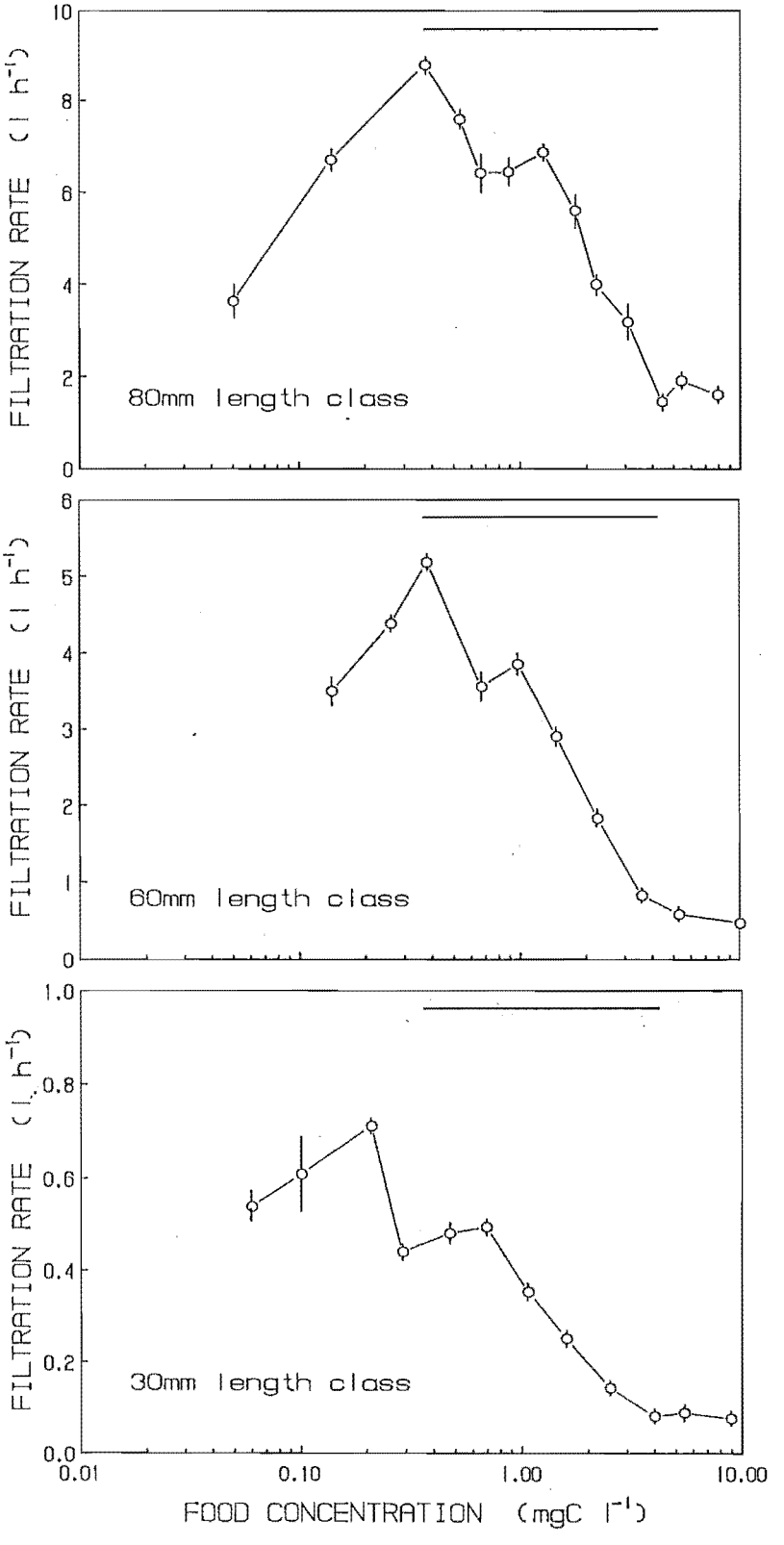

Figure 1. Changes in filtration rate by Perna canaliculus *of 3 length classes at different food concentrations. Horizontal bars show the range of concentrations of food occurring within mussel farms in Marlborough. Vertical bars show 95% confidence intervals.*

concentration up to 1.1 mgC l^{-1} food (Fig 2), above this threshold reduced filtration rate maintained the ingestion of a maximal ration and the feeding behaviour was different in this fundamental respect. The results are therefore presented as complex curves comprised of five different phases.

Type 1 feeding activity occurred below 0.4 mgC l^{-1} *I. galbana* (21,000 cells ml^{-1}). As food concentration increased from 0.05 mgC l^{-1} filtration increased from low values at low food concentrations to maximal rates. Maximal filtration rates were recorded at food concentrations of 0.021 mgC l^{-1} (30mm length class) to 0.38 mgC l^{-1} food (60mm and 80mm class). Faeces which were produced during type 1 feeding were thin in cross-section, and tended to split along the anal groove.

At maximum recorded filtration rates, ingestion rates of 0.004 gC d^{-1} (30mm length class), 0.054 gC d^{-1} (60mm class) and 0.081 gC d^{-1} (80mm class) were recorded, and ingestion rate therefore increased 20-fold as mussels increased in length 2.7 times (Fig 2). At maximum filtration rate, mussels of different size classes ingested from 41% to 57% of their maximal ration (see below).

During type 2 feeding, filtration declined significantly to 68-73% of these maximal rates. Nevertheless, increases in food concentration compensated for these reductions in filtration rate, and the rations ingested by mussels of all size classes

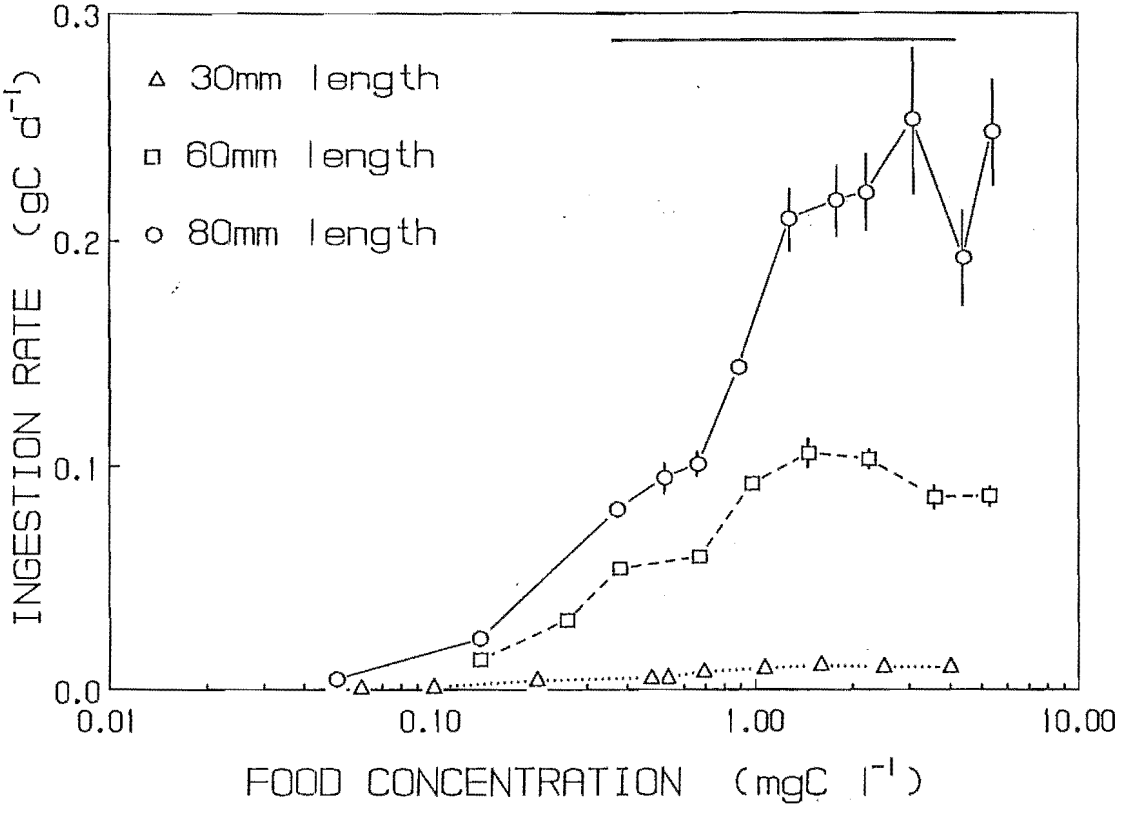

Figure 2. Changes in ingestion rate by 3 length classes at different food concentrations. The horizontal bar indicates the range of concentrations of food occurring within the mussel farms of Marlborough. Vertical bars show 95% confidence intervals.

therefore increased progressively as food concentration increased. Faeces produced during this mode of feeding were thicker in cross-section and split along anal grooves less often than those collected during type 1 feeding.

Type 3 feeding behaviour occurred between 0.4 and 1.4 mgC l^{-1} food, and occurred at slightly lower minimum food concentrations in the 30mm length class (0.46 mgC l^{-1}) than in either the 60mm or 80mm classes (0.66 mgC l^{-1}). During type 3 feeding, filtration within each length class of mussels were similar at different food concentrations, and mussels of a given length filtered at similar rates until increased food concentration supplied the mussel with its maximum ration.

Type 4 feeding behaviour occurred above lower thresholds within the range 1.1-1.4 mgC l^{-1} food in each size class. During type 4 feeding, filtration rate decreased as food concentration increased, and this decline in filtration caused a consistent and maximal ration to be ingested within each length class. During this mode of feeding, less food than this maximal ration was ingested at higher food concentrations (>2 mgC l^{-1}) only when older cultures of algae were used as food. Maximum ration increased from 0.008 gC d^{-1} in the 30mm length class to 0.23 gC d^{-1} in the 80mm class (Fig 2); regression analysis indicated that this maximal ration increased in proportion to mussel length raised to the power of 3.01 (r^2=0.99, F-test, $p<0.01$). However, mussels of different length classes ingested their different maximal rations over similar ranges of food concentrations. Maximal rations were ingested from:

1.1-4.0 mgC l^{-1} by mussels of 30mm length,

1.4-3.6 mgC l^{-1} by mussels of 60mm length, and

1.3-4.4 mgC l^{-1} by mussels of 80mm length.

Faeces produced by mussels ingesting their maximal ration were thick in section, had deep and distinct anal grooves, and were quite friable. It should be noted that faeces were protected by a fluted faecal trap (Section 3.1), and did not fragment or otherwise loose their structure within the the experimental chamber.

Type 5 feeding behaviour occurred from food concentrations of 4 to 10 mgC l^{-1}, when minimal filtration rates ranging from 0.08 to 1.7 l h^{-1} were recorded within the three length classes. Within each length class, mussels filtered at similar rates at different concentrations of food. Substantial volumes of pseudofaeces containing undigested algae were ejected during type 5 feeding. Ejected faeces were thick and friable, and contained well digested algae. This partitioning of captured algae between faeces and pseudofaeces was not determined, preventing ingestion rates from being calculated during this mode of feeding. As defaecation rates were similar during both types 4 and 5 of feeding, however, it is most probable that mussels ingested their maximal rations above a food concentration of 4 mgC l^{-1} and that the surplus food captured was rejected as pseudofaeces.

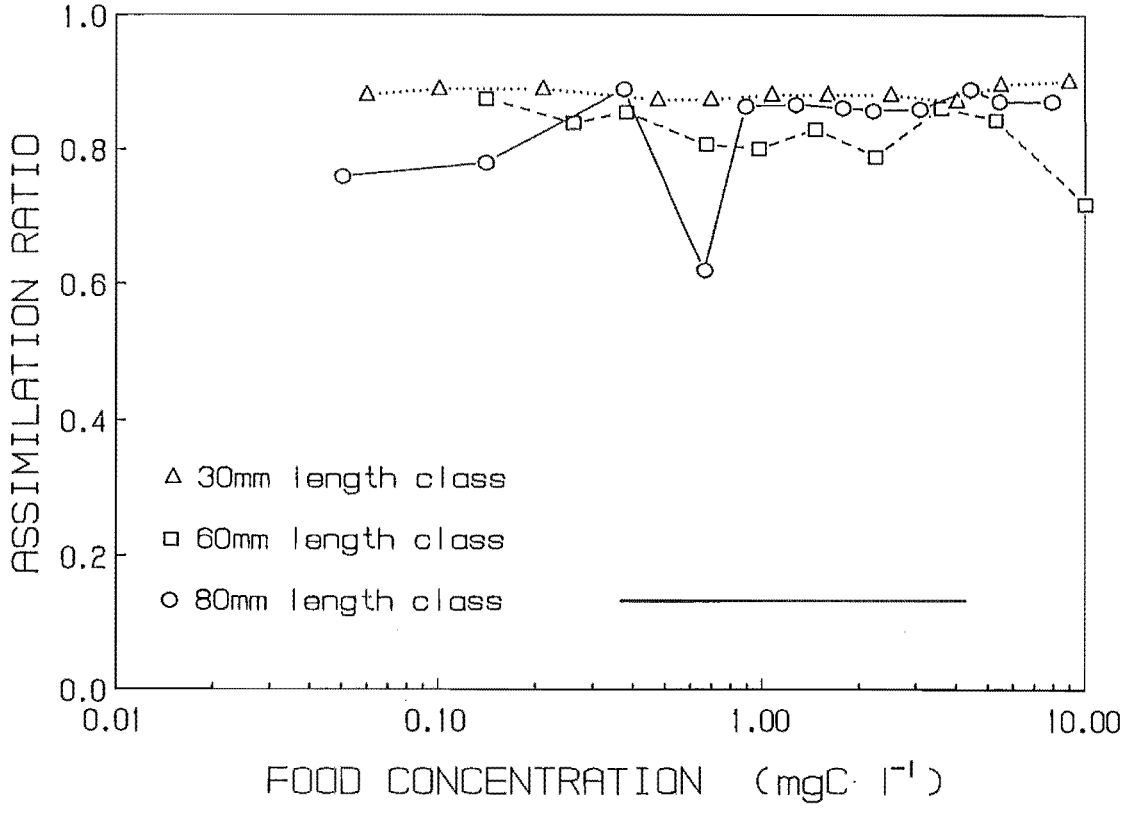

Figure 3. Changes in assimilation efficiency by P. canaliculus *of three length classes as food concentration increased. Horizontal bar indicates the range of food concentration in mussel farms.*

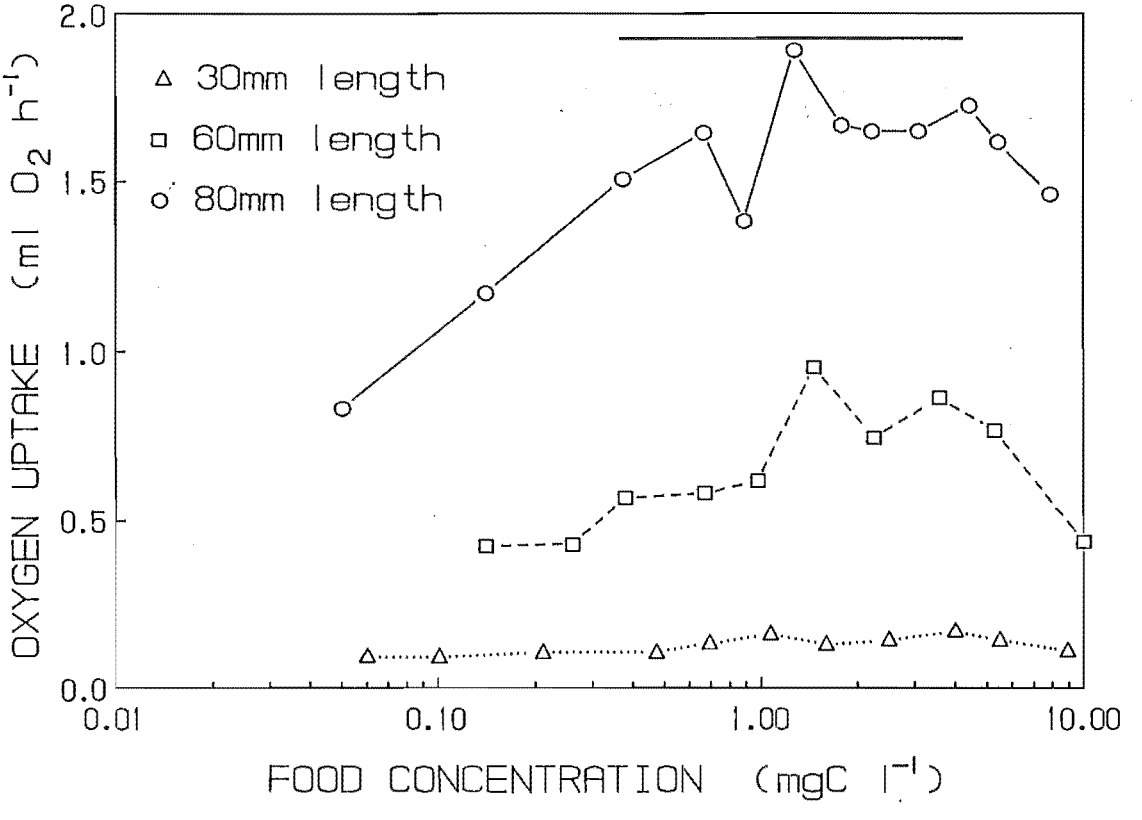

Figure 4. Changes in oxygen uptake by P. canaliculus *of three length classes of mussels as food concentration increased. Horizontal bar shows food concentration in mussel farms.*

Uptake of Carbon

Estimates of assimilation efficiency derived using Conover's (1966) method were consistently high (>96%) compared with those determined using total carbon collection methods (82-89%), suggesting that inorganic matter was assimilated by *P. canaliculus*. Values were therefore corrected using the technique of Bjorndal (1985). Assimilation efficiency did not vary significantly between similar sized mussels ingesting different rations (ANOVA, $F=0.86$, $df=10$, $p=0.58$; Fig 3). It is concluded, therefore, that marked increases in ration due to increased food concentration affected energy uptake more than minor changes in digestive efficiency. Tukey's test also indicated that mussels of 30mm length may have assimilated more organic matter from food (AE=89%) than did larger mussels (AE=82-83%, $p<0.05$). However, these differences were not marked, and when a single case was omitted from the data set (80mm length class, 0.7 mgC l^{-1} food) my results indicated that the 80mm and 30mm length classes may digest food at similar, high efficiencies.

Oxygen Uptake

In all three length classes, oxygen uptake of each mussel decreased as ingestion rate increased with food concentration (regression analysis, $p<0.004$; Table 1, Fig 5). Of the variance in oxygen uptake, 68-74% could be attributed to changes in ingested ration, but higher regression coefficients obtained for small mussels indicated that their oxygen uptake decreased more rapidly as their ration declined than in larger mussels (Table 1).

While filtration declined markedly in mussels ingesting a maximal ration, oxygen uptake did not decline noticeably as filtration declined. The energy required for filtration did not therefore appear to comprise a major respiratory cost to mussels during type 4 feeding.

Oxygen uptake per gram body weight was greater in mussels of greater length and maturity (ANOVA, $F=149$, $df=2$, $p<0.0001$), and increased in mussels of similar size

Table 1. The regression of oxygen uptake (ml O_2 h^{-1}) against ingested ration (10^8 cells h^{-1}) in mussels of 30, 60 and 80mm length.

LENGTH CLASS	REGRESSION CONSTANT	REGRESSION COEFFICIENT	SIGNIFICANCE (F-test)	VARIANCE EXPLAINED
30 mm	0.078	+0.264	0.002	71%
60 mm	0.316	+0.214	0.003	74%
80 mm	1.092	+0.127	0.004	68%

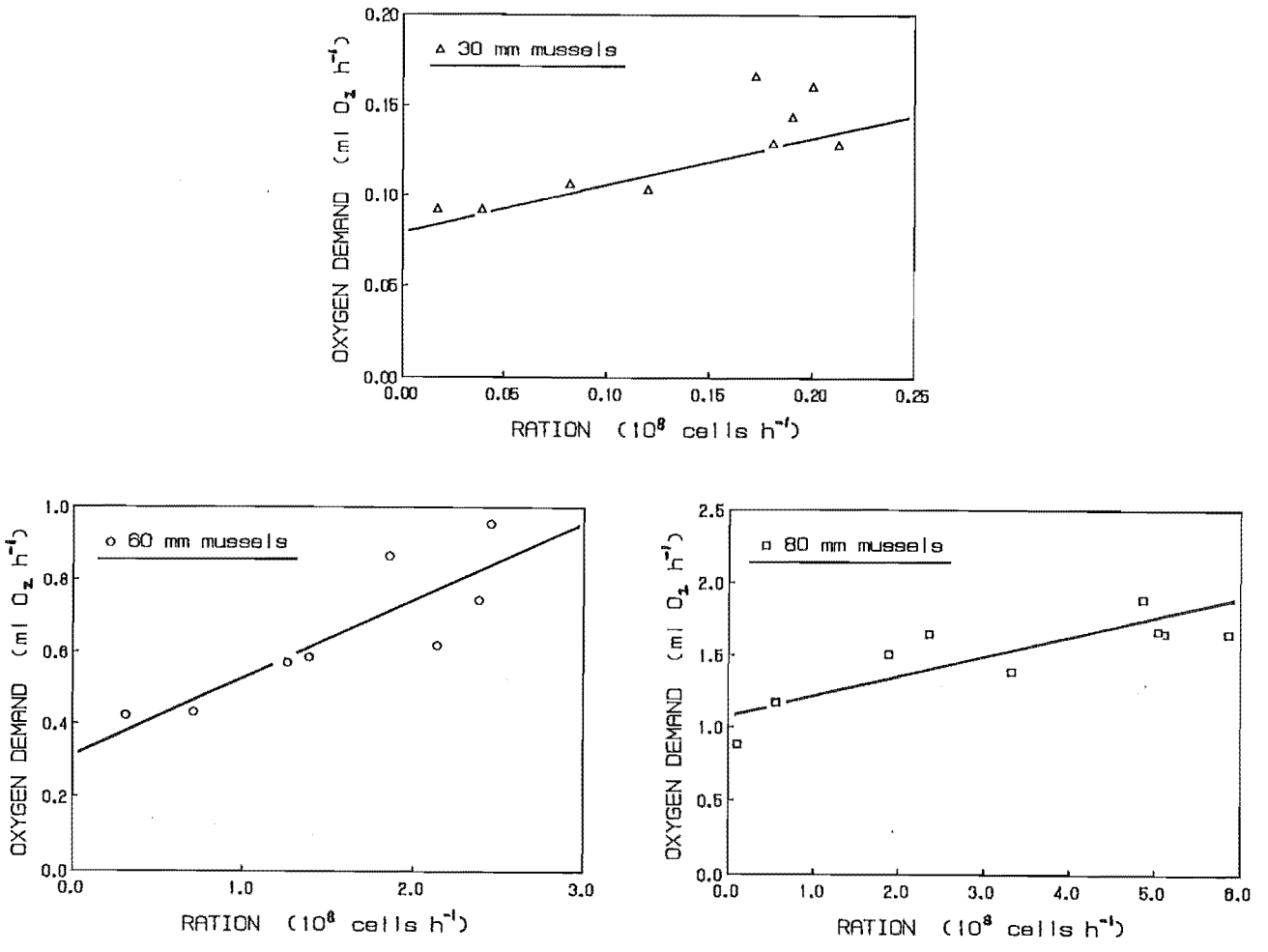

Figure 5. Relationships between ingested ration and respiration rates for three different length classes of P. canaliculus.

ingesting more food (ANOVA, $F=6.14$, $df=9$, $p<0.001$). While ingesting a maximal ration, the immature 30mm length class took up 1.4 ml O_2 g^{-1}DW, whereas the mature mussels comprising the 60 mm and 80mm classes took up only 0.6 ml O_2 g^{-1}DW and 0.5 ml O_2 g^{-1}DW, respectively.

Temporal Consistency of Ingested Ration

Temporary deprivation of food at times when oxygen uptake was determined caused the feeding behaviour of mussels to change. When mussels were exposed to less than 1 mgC l^{-1} food after respirometry (types 2-3 feeding), they adapted to the renewed supply of food within one hour, after which they filtered at high rates. Ingestion rates stabilised at low rates soon after feeding recommenced, and ration was limited by availability of food at these low food concentrations. At high food concentrations typically inducing type 4 feeding behaviour within stable feeding regimes, however, full adaptation to the renewed supply of food took a substantially longer period of 2-5 hours.

In mussels of 80mm length, rapid filtration at rates similar to those recorded during type 3 feeding was recorded until mussels began adapting to the renewed presence of food (Table 2). By comparison, while mussels of 30 and 60 mm length filtered more rapidly after minor disturbance, their initial feeding rates were less than those recorded during type 3 feeding. After protracted exposure to food, filtration by 30 and 60mm length mussels declined by 25-64% to even rates characteristic of type 4 feeding. Mussels therefore responded to a temporary reduction in food intake by tripling their food intake for a period lasting 2-5 h.

Table 2. Differences between initial and final, stable filtration rates ($l\ h^{-1}$) during type 4 feeding (1 - 4 mgC l^{-1} food concentration).

APPROXIMATE CONCENTRATION OF FOOD	80 MM SIZE CLASS		60 MM SIZE CLASS		30 MM SIZE CLASS	
	INITIAL FR	FINAL FR	INITIAL FR	FINAL FR	INITIAL FR	FINAL FR
1.1 mgC l^{-1}	6.39	6.78	*	3.85	0.51	0.34
1.6 mgC l^{-1}	7.42	5.56	*	2.45	*	0.24
2.3 mgC l^{-1}	6.87	4.00	3.74	1.83	0.30	0.14
3.4 mgC l^{-1}	7.02	3.20	2.32	0.88	0.22	0.08

* initial food concentration too high to determine filtration rate

Energy Transfer Processes

Mussels of all sizes showed transitions from negative to positive Growth Potential (GP) at 0.1-0.2 mgC l^{-1} food (Fig 6a,b,c). GP then increased with ingestion rate until maximum ingestion occurred. Mussels of the 30mm length class ingested maximal ration and attained maximum GP at only 64% of the food concentration required by larger mussels. Thus, 30mm long mussels had higher GP at 1.0-1.4 mgC l^{-1} food (intermediate concentrations) than did larger mussels of the 60 and 80mm length classes.

Whereas 30mm mussels ingested more carbon per gram body weight than larger mussels (ANOVA, $F=13.8$, $df=2$, $p<0.001$), they respired greater proportions of the carbon they assimilated. Respiration accounted for from 21% (80mm length) to 49% (30mm length) of the energy assimilated by mussels. The higher carbon uptake of 30mm long mussels was therefore offset by higher expenditure of energy by these small mussels, and so mussel length did not affect GP markedly at condition indices sampled during this study (ANOVA, $F=2.96$, $df=2$, $p=0.08$). Similar maximal GP of 3.7, 4.0 and 4.1% body C d^{-1} were recorded for mussels of 30, 60 and 80mm length, respectively, under conditions of maximal ingestion.

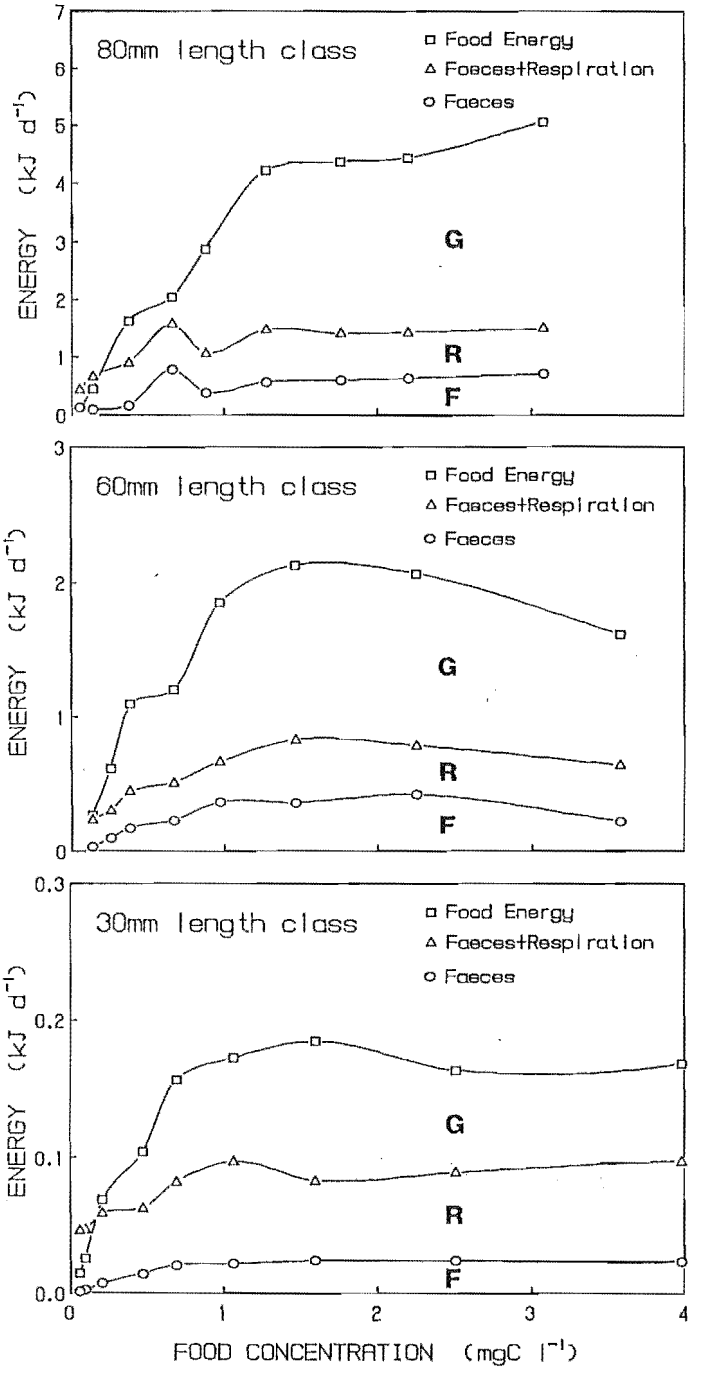

Figure 6. Energy budgets calculated for 3 length classes of mussels at different concentrations of food (G=Growth Potential, R=respiration, F=faeces).

conditions of maximal ingestion.

After correction for natural variation in condition (see methods), 80mm length mussels were calculated to have a GP which was 3.0 times higher than 30mm length mussels with a condition index of 8% (Table 3). At 12% condition index, mussels of all sizes had markedly lower calculated GP than mussels of similar length but lower condition, and calculations indicated that 30mm length class mussels had negative GP even when ingesting maximum ration. These small mussels do not and, perhaps cannot attain such high condition in nature. Results, however, indicated that natural declines

Table 3. Estimates of maximum Growth Potential (% body energy d^{-1}) in P. canaliculus *of different length and condition index. [Condition index = (tissue weight/total weight) * 100]*

MUSSEL	STANDARD CONDITION INDEX		
LENGTH (mm)	8%	10%	12%
30	1.79	0.43*	-0.23*
60	4.99	3.71	2.86*
80	5.42	4.09	3.25

*: condition rarely occurred in nature

in the condition of adult mussels from 13% to 7% (Section 2) may allow a greater fraction of the mussels energy uptake to be used for growth.

While mussels ingested a maximal ration, both Gross Growth Efficiency (GGE) and Net Growth Efficiency (NGE) varied between 30mm length mussels and efficiencies for the 60 and 80mm mussels (ANOVA, $F>17.9$, $df=2$, $p<0.004$). In all 3 length classes, zero growth was calculated at 0.1-0.2 mgC l^{-1} food, however, and GGE then increased to maxima of between 0.48 (30mm length) and 0.66 (80mm length) while mussels ingested their maximum ration. NGE also increased to maxima of between 0.54 (30mm length) and 0.76 (80mm length) at maximum ration.

At all food concentrations, 11 to 18% of the carbon ingested was lost in faeces by mussels of 30-80mm length. The quantity of faeces produced was strongly dependent on both the length of mussels and food concentration. In addition, marked production of pseudofaeces occurred above concentrations of 3.6-4.4 mgC l^{-1} food, and the quantity of pseudofaeces produced then increased rapidly with food concentration. Interactions between food concentration, mussel size and stock density were therefore primary determinants of both the carbon retained within a mussel community, and the carbon transferred to adjacent communities.

DISCUSSION

Feeding Behaviour in Long-Term Experiments

Mytilus may show three different patterns of feeding behaviour at different concentrations of food. They may cease to feed at very low food levels, filter at high and constant rates at intermediate food levels, and reduce filtration effort at high food concentrations (eg Winter 1978a; Navarro and Winter 1982). *P. canaliculus* showed a complex filtration curve which was comprised of five different feeding behaviours, described as numbered phases to facilitate discussion.

Mussels may only feed above a minimum threshold food concentration (type 1 feeding). Such threshold feeding was predicted in mussels at only 10% of food concentrations (Navarro and Winter 1982; Winter 1978a) that this threshold occurred at in *P. canaliculus*. A similar threshold also occurred in *M. edulis* at only 25% of the food concentration recorded in *P. canaliculus* (Riisgard and Randlov 1981). Changes in concentrations at which feeding thresholds occur indicate that changes in dietary control mechanisms may occur between different species of mussel.

Type 2 feeding appears atypical of other mussels, but could be explained by variation of dietary regulation between mussel species. The adaptive significance of this feeding behaviour may occur within declining food resources when enhanced filtration results in a slow decline of ingestion rate as food concentration decreases, and this enhancement of filtration rate appeared to delay the onset of nutrient deficiency in the presence of declining food resources. Enhanced type 2 filtration occurs at all three mussel lengths, as food concentration increases and decreases, and during ratification after studies on each size class had been completed. Smooth curves could not be fitted within 95% confidence intervals of data describing filtration by any length class of mussels. The persistent occurrence of type 2 feeding indicates that this behaviour was not an artifact of technique.

Above 0.6 mgC l^{-1} food, feeding by *P. canaliculus* resembled that of other bivalves studied within temporally stable environments. These moderate to high concentrations of food are typical of those found in mariculture systems (Section 2). Thus, types 3 to 5 of feeding may occur more frequently in cultivated mussels.

During type 3 feeding, *P. canaliculus* filtered at consistent, high rates until increased food availability supplied grazers with full ration at intermediate food levels. In other mussels, such as *M. chiliensis*, high uniform filtration rates occurred until filtration rates became regulated at high food concentrations (Winter 1978a; Navarro and Winter 1982). Such a feeding behaviour appeared to be identical to the type 3 feeding recorded in *P. canaliculus*.

The most important feeding threshold occurs at food concentrations of 1.0-1.4 mgC l^{-1} when mussels commenced type 4 feeding. Whereas food availability limits food uptake below this threshold, ingestion was maximal at higher concentrations. *P. canaliculus* limited food intake by reducing filtration rates at higher food concentrations, and this mussel therefore showed a change in feeding behaviour consistent with that observed at similar food concentrations (1.4-1.8 mgC l^{-1}) in the field (Section 2.2). Analogous control of ingestion by limiting filtration is known for a number of other mussels (Winter 1969; 1973; 1978a; Riisgard and Randlov 1981; Navarro and Winter 1982; Sprung 1984b) and bivalves (see Epifanio 1981; Winter 1969) fed at high concentrations of food.

However, the food concentration threshold at which maximal ration was first ingested, and above which filtration declined, appears to vary markedly between bivalve species. Whereas larvae of *M. edulis* ingested a maximal ration at only 0.2 mgC l^{-1} *I. galbana* (Sprung 1984b), 25mm length *M. edulis* first ingested a maximal ration at 0.5 mgC l^{-1} *Phyodactylum tricornutum* (Riisgard and Randlov 1981). However, the oyster *Crassostrea virginica* ingested a maximum ration above 5 mgC l^{-1} *I. galbana* (Epifanio and Ewart 1977). By comparison, 30-80mm length *P. canaliculus* ingested maximum food above 1.1-1.4 mgC l^{-1} *I. galbana*, and either interspecific, developmental, or food specific changes in this threshold occur inducing variation in feeding behaviour between studies using different bivalves.

Effects of Experiment Duration

For the purposes of the present discussion, experiment duration is defined as the time elapsed between when animals are placed in the experimental chamber (or feeding is subsequently interrupted or disturbed) and when their feeding rates are determined. It should be noted that this period is exclusive of acclimation when animals are held in a separate system prior to the measurement of filtration rate.

Reduced filtration is not recorded in experiments which were conducted on *P. canaliculus* for less than two hours, and short-term studies on *M. edulis* also show little variation in filtration between different food concentrations (Thompson and Bayne 1974; Bayne and Worral 1980; Widdows 1978a). In contrast, long-term feeding studies indicate that filtration by *M. edulis* becomes strongly limited at high concentrations of food (eg Winter 1973; Schulte 1975; Sprung 1984b). Similar differences are also apparent when other feeding studies are compared. While filtration rate was not limited at high food concentrations during short-term experiments on other mussels and bivalves (eg Rodhouse 1978; Griffiths and King 1979; Griffiths 1980), filtration declined markedly at high food concentrations during studies lasting over 10 hours (Epifanio 1981; Navarro and Winter 1982; this study). Such differences occur even between studies on a single species of mussel (*M. edulis*), and are not easily explained (p121: Widdows 1978a). There is, however, an interesting accord between the duration of the above experiments and the feeding behaviours recorded.

Both *M. edulis* (Riisgard and Randlov 1981; Sprung 1984b) and *P. canaliculus* (Section 3.1; this study) filtered rapidly for three hours after being resupplied with high concentrations of food, but filtration rates then decreased to markedly lower, stable rates over several hours. This transition of filtratory behaviour over time did not occur at low food concentrations, but filtration declined by 64% (this study) to 69% (Sprung 1984b) of maximal filtration rates after mussels had fed at high food concentrations for over 3 hours. Similarly, retention efficiency and pumping rates of *Ostrea edulis* also

declined markedly during long-term (55 hour) experiments conducted at food concentrations exceeding 10^5 cells ml^{-1} *I. galbana* (Wilson 1983). Long-term feeding studies therefore may be required to describe feeding behaviour under the conditions of constant and high concentrations of food.

A classic short-term study by Thompson and Bayne (1974) indicated that *M. edulis* consumed an excessive ration at high food concentrations, so limiting carbon uptake and growth. Similar results were reported from comparable studies on other mussels (Griffiths and King 1979; Griffiths 1980). While short studies suggest that growth declines at high food concentrations, long-term experiments on *M. edulis* (Riisgard and Randlov 1981; Sprung 1984a) and other mussels (Navarro and Winter 1982; this study) indicate that filtration declines at high food concentrations. This behaviour had the effect of regulating diet, and thus maintaining carbon uptake and growth in the presence of abundant food.

The above differences may result due to intra- and inter-specific variations, ontogenetic change and specific adaptations to divergent environments (Widdows, Pers Comm). However, in some populations, at least, of both *M. edulis* and *P. canaliculus*, feeding behaviour changes as a function of time alone. Beneficial adaptation does not explain why the net energy uptake of mussels can decline at high food concentrations during experiments of short duration (below). Therefore, it is seems necessary that possible impacts of experiment duration on feeding be determined for each different population of mussels studied. In the absence of such primary data, long-term (>20h) experiments should be conducted.

My long-term experiments provide predictions of growth consistent with the growth of bivalves in relatively stable, field environments (Section 2), and describe feeding behaviours that are adapted to utilise a stable food resource efficiently.

Digestion of Food

Regulation of filtration may limit ingestion rate and maintain digestive efficiency at high concentrations of food. Three independent studies (Riisgard and Randlov 1981; Sprung 1984a; Section 3.1) show mussels can ingest unusually large volumes of food when exposed to high food concentrations after food deprivation. *P. canaliculus* ingested up to 3.0 times more food after feeding was interrupted during oxygen uptake studies, but it is debatable whether these large volumes of food were digested efficiently.

A maximal regulated ration of 7-9 mgC d^{-1} was taken by both 100 mgDW *M. edulis* (Riisgard and Randlov 1981) and 100 mgDW *P. canaliculus* (this study) during extended feeding studies. However, *M. edulis* of this size did not regulate ingestion rate during short feeding experiments and assimilation efficiency declined from 90 to 20% as

ration increased to 25 mg d^{-1} (Thompson and Bayne 1974); assimilation efficiency also fell 3.3 times as ration increased to 36 mgC d^{-1} (Widdows 1978a). Data of both Thompson and Bayne (1974) and Widdows (1978a) indicates that while *M. edulis* ingested less than the regulated ration of 7-9 mgC d^{-1}, *M. edulis* assimilated 74-76% carbon from *P. tricornutum*. Thus, control of diet volume may induce a four-fold increase in digestive efficiency.

Feeding studies of short duration have shown that unregulated intake of food was associated with reduced assimilation efficiency (*M. edulis*: Thompson and Bayne 1974; Widdows 1978a; *Aulacomya ater*: Griffiths and King 1979; *Choromytilus meridionalis*: Griffiths 1980), and energy budgets derived from these four studies suggest that reduced digestive efficiency had limited growth or growth efficiency at high food levels. Alternatively, reduced assimilation could result from an over-consumption of food. This speculation was subsequently supported by observations that assimilation efficiency in *M. edulis* probably declines at unstable and high concentrations of natural foods when filtration did not appear to have been regulated (Frechette and Bourget 1987). While analogous superfluous feeding coupled with reduced digestive efficiency can occur in copepods, Morales (1987) indicates that superfluous feeding does not occur in certain copepods fed at stable food concentrations. The observations of reduced energy uptake at high food concentrations in short-termed studies may therefore, in some instances, be artifacts of experimental designs which allow insufficient time for mussels to adapt to a new environment.

If digestive efficiency does not decline at unusually high ration levels, then *M. edulis* may optimise uptake of patchily distributed food by increasing ingestion after food deprivation (Sprung 1984b). If digestive efficiency falls at high ingestion rates, however, then energy uptake may be both food limited at low food concentrations and become limited by low digestive efficiency if the abundance of food increases too much, and too rapidly.

In stable feeding regimes, ration did not affect the digestion of foods so markedly. *P. canaliculus* digested *I. galbana* efficiently (82-89%) at all the food concentrations tested during this study, and assimilated 81% carbon from natural foods (Section 2.2). In 27 of 32 studies cited by Winter (1978b), 60-94% of algal carbon was assimilated, and net carbon uptake from *P. tricornutum* (*M. edulis*: Riisgard and Randlov 1981) and *Dunaliella marina* (*M. chiliensis*: Navarro and Winter 1982) was maintained as both food concentration and ingestion rate increased. In *P. canaliculus*, neither assimilation efficiency nor carbon uptake declined at high concentrations of food. Most food that was ingested by *P. canaliculus* was digested efficiently.

Energy Balance

Growth potential was determined by the balance between food uptake, and respiratory and excretory losses (Crisp 1984). In *Perna canaliculus*, both energy uptake and respiration losses were dependent on the quantity of food digested, and ingestion rate was therefore a primary determinant of Growth Potential. However, as anaerobic metabolism was not measured in this study, and growth energy is also used for reproduction, my estimates of growth potential can overestimate somatic growth.

Growth can induce change in the optimal growth environment and affect productivity (Ross 1981a,b; Schiemer 1985). Some studies suggest that smaller proportions of assimilated energy are available for growth as mussels increased in size (eg Griffiths and King 1979; Navarro and Winter 1982; Thompson and Bayne 1974), but such a trend was not apparent in *P. canaliculus* where simple differences in Growth Potential did not occur between length classes. The higher weight specific respiration of small mussels, coupled with reduced somatic energy reserves may, however, make them vulnerable to starvation during periods of reduced food resources. But small, immature mussels consumed larger fractions of their maximal ration as food concentration increased than did larger mussels. These 30mm length mussels also ingested their maximal ration at only 70% of the food concentration required by the 80mm length class. Immature mussels may therefore grow more rapidly at 0.3-1.2 mgC l^{-1} food but, once maximal ration was ingested, all length classes showed similar growth potential. Mussels of different length therefore may have different optimal levels of food, and compete against coexisting animals more successfully over different ranges of food concentrations.

While high condition index reflects the availability of nutrient reserves which can be utilised during periods of low carbon uptake, increased body mass also increases respiration losses and so reduces growth potential. Whereas adults of high condition should produce more gametes during spawning events, the low condition and body mass of immature mussels may reduce their respiratory losses. Thus, ontogenetic variation in optimal condition probably occurs. In juvenile mussels, success is enhanced by rapid somatic growth until reproductive size is reached, whereas mature mussels may best improve success by using energy to increase their gamete production.

Indices of growth efficiency provide a measure of the proportion of energy in food available for growth plus reproduction. Growth efficiency increased with mussel size, and net growth efficiency (NGE) increased with ingestion rate to maxima of 0.54 (30mm length mussels) and 0.66 (80mm length). *M. edulis* attained maximal NGE of 0.61 at 20mm length (Riisgard and Randlov 1981), a figure comparable with that of 30mm length class *P. canaliculus* (0.54). Also, in *M. chiliensis* net growth efficiency declined by 18% as mussels grew to 1.5 gDW (Navarro and Winter 1982), an opposing trend to that in

P. canaliculus. My 95% confidence intervals suggest errors in determining diet (±6%), assimilation efficiency (±4%) and oxygen uptake can obscure minor changes in growth efficiencies between mussel species. Ontogenetic variations in energy flow may also occur that affect growth. Given this range of factors affecting estimates of growth efficiency, the above studies provided consistent estimates of growth efficiency in different species of mussels that ingested a maximal ration of moderate or high quality foods.

Whereas short-term feeding experiments predict reduced growth at both low and high food concentrations, long-term studies indicate that diet is regulated (Winter 1973, 1978a) and growth is maximal at high food concentrations (eg Navarro and Winter 1982; Riisgard and Randlov 1981; this study). These long-term studies therefore suggest that patterns of nutrition and growth in bivalves may be more consistent than the results of some short-term dietary studies indicate (Epifanio and Ewart 1977; Widdows 1978a; Winter 1978b). The results of my study support the conclusion that energy balance of mussels is positive over a wide range of food concentrations (Navarro and Winter 1982). Mussels grew most rapidly while food was abundant in the field (Section 2), and growth potential of *Perna canaliculus* was maximal at the similar, high concentrations of food used in this laboratory.

SECTION 3.2.2.

Impacts of temperature and food availability on nutrition and growth potential in the mussel Perna canaliculus

ABSTRACT

Temperature and food concentration were varied within the ranges 12-18°C and 0.05-10.8 mgC l^{-1}, respectively. Determinations were made of the effects of these factors on the feeding behaviour and energy budgets of mussels of 80mm length.

At 18°C the pattern of feeding was similar to that previously described for 15°C. Five types of feeding behaviour occurred as food concentration increased to 10 mgC l^{-1}. 1. Filtration rate increased from 0.05 to 0.4 mgC l^{-1} food. 2. As food concentration increased further, filtration declined to 73% of maximum rates. 3. Uniform filtration occurred until increased food availability provided mussels with a full ration. 4. Above 0.9-1.4 mgC l^{-1}, filtration decreased further whereas ingestion remained maximal. 5. Above 3.2-4.4 mgC l^{-1}, mussels filtered at minimal rates and produced pseudofaeces.

At 12°C, in contrast, filtration increased to a maximal rate at the higher concentration of 0.7 mgC l^{-1} food. In addition, no significant decline in filtration occurred until mussels ingested at least 91% of their maximal ration. Thus, the second and third modes of feeding behaviour listed above were not recorded at 12°C.

Maximal ingestion rates increased by 64% as temperature increased from 12° to 15°C. Maximal ingestion rates were similar at both 15° and 18°C. The maximal ration of food ingested by mussels was inversely proportional to gut passage time, indicating that digestive factors may limit the maximal amount of food consumed. However, assimilation efficiency was not dependent on either ration or water temperature.

Mussels attained zero growth at 0.12-0.18 mgC l^{-1} food. "Scope for Growth" then increased with ration to maximal rates of 4.1% (12° and 15°C) to 5.8% (18°C) body C d^{-1}. To grow at maximal rates mussels may require 60% higher food concentrations (1.4 mgC l^{-1}) at 15°C compared with the food needed to grow rapidly at either 12° or 18°C.

INTRODUCTION

For most organisms, including mussels, there are likely to be optimal conditions of temperature and food concentration which may enhance their growth in natural, cultivation and hatchery rearing systems. This part of the study assessed food intake and

energy flow over a range of temperature and food concentrations in an attempt to define growth optima for adult *P. canaliculus*.

Previous experiments have indicated that low food concentration limits both food intake and growth by mussels (Navarro and Winter 1982; Riisgard and Randlov 1981; Sprung 1984a,b), and therefore affect the production and reproductive output of mussel communities. In separate studies, feeding has been shown to increase with temperature (eg Malouf and Breese 1977; Schulte 1975; Wilson and Seed 1974) and to be inhibited above 20°C (Widdows 1973). Digestive, respiratory (Bayne 1976; Griffiths 1980) and growth factors (Shumway and Newell 1984; Sprung 1984b,c) also vary with temperature and determine the availability of carbon for growth.

Because such factors may vary differently at each temperature and food level studied, it is necessary to conduct experiments over the range of both factors sampled in the field. Only two authors (Walz 1978a,b; Sprung 1984a,b,c, 1985) have shown how feeding and growth of mussels varied with contemporaneous changes in food concentration and temperature. This study addresses the question of how *P. canaliculus* is affected by successions in temperature and food availability.

Marked changes in condition and growth of bivalves (Beukema et al. 1976; Hummel 1985b; Rainer 1985) including *P. canaliculus* (Section 2.1) occur between sites and over time. Temperature and food concentrations also vary between sites and over time, and regression analysis suggests that both factors determine spatio-temporal changes in feeding and growth (Section 2.2). Experimental determination of energy budgets are needed, however, both to suggest whether such interaction does occur, and to indicate how site, season and situation affect the mussel's biology.

MATERIALS AND METHODS

Determination of Feeding and Energy Budget

Three groups of eight mussels, 80mm in length, were collected from Mahanga Bay. At the times of collection, temperatures in the bay ranged from 14 to 17°C. Mussels were acclimated for 14 days at each of three temperatures (12°, 15° and 18°C). During this period, mussels were fed *Isochrysis galbana* and maintained at a salinity of 34 ppt. Each group of 8 mussels was then placed in experimental apparatus described in Section 3.1, and provided with *I. galbana* at 9 to 12 different concentrations in the range of 0.05-10.8 mgC l^{-1} food, and in water at their acclimation temperature. Filtration rate, food intake and oxygen uptake were measured for each group of 8 mussels at one temperature and all food concentrations, using those methods described in Sections 3.1 and 3.2.1. Determinations were made on a single group of eight mussels at each

temperature, and feeding was recorded every 40 minutes overnight and after feeding rates had stabilised. Error was assessed using results obtained during at least 18 consecutive time periods. After each experiment was completed, the mussels comprising each experimental group were measured, weighed and then combusted (see Section 3.2.1).

Measurement of Gut Passage Times

Radiotracer pulse techniques are recommended for determining gut passage times of continuous feeders by Duncan and Klekowski (1975), and are used in this study. Passage times of eight 80mm length mussels were measured at temperatures of 12.5, 14.8, 16.5 and 18.9^{o}C. The mussels used had been acclimated for five days before use in experiments. Mussels were pre-fed unlabelled *I. galbana* (1.8 mgC l^{-1} food) for 4 hours, and this allowed their digestive tracts to fill with food before experiments began.

I. galbana (1.8 mgC l^{-1} food) was labeled with 50 uCi Chromium-51, a non-assimilated tracer (Calow and Fletcher 1972), and fed to mussels for 20 minutes. Mussels were then moved to another aquarium (100 l volume) and fed unlabelled *I. galbana* at the same concentration while suspended above faecal collection trays. Faeces were collected every 20 or 30 minutes using a pipette, over a period of 8 to 10 hours. A final collection of faeces was made 20 hours after the inoculation of labeled algae.

Faeces were dried, solubilised (Mahin and Lofberg 1970), and then counted using a Phillips 4700 series Liquid Scintillation Counter and a triton X-100/PPO scintillation cocktail. Counts were corrected to DPM using a channels ratio quench correction curve. The time taken to defaecate 50% of the ingested Chromium-51 (GPT_{50}) was then calculated.

RESULTS

Feeding Behaviour

At both 18^{o} and 15^{o}C, filtration rate increased to maxima of 13.4 and 8.8 l h^{-1}, respectively, as food concentration increased from 0.05 to 0.40 mgC l^{-1} *I. galbana* (Fig 1). This behaviour resembled type 1 feeding (see Section 3.2.1), and also occurred in mussels feeding at 12^{o}C. Maximum filtration rates occurred at 0.40 mgC l^{-1} food at and above 15^{o}C, but occurred at the substantially higher concentration of 0.7 mgC l^{-1} food at 12^{o}C.

At 18^{o} and 15^{o}C, filtration declined to 74% of maximum recorded rates as food concentrations increased to 0.6 mgC l^{-1} (type 2 feeding, Section 3.2.1). Mussels then filtered at constant rates until increasing food concentrations enabled them to collect a maximum and stable ration (type 3 feeding, Section 3.2.1). At 12^{o}C, however, types 2 and 3 of feeding were not seen, and maximum filtration occurred at a substantially

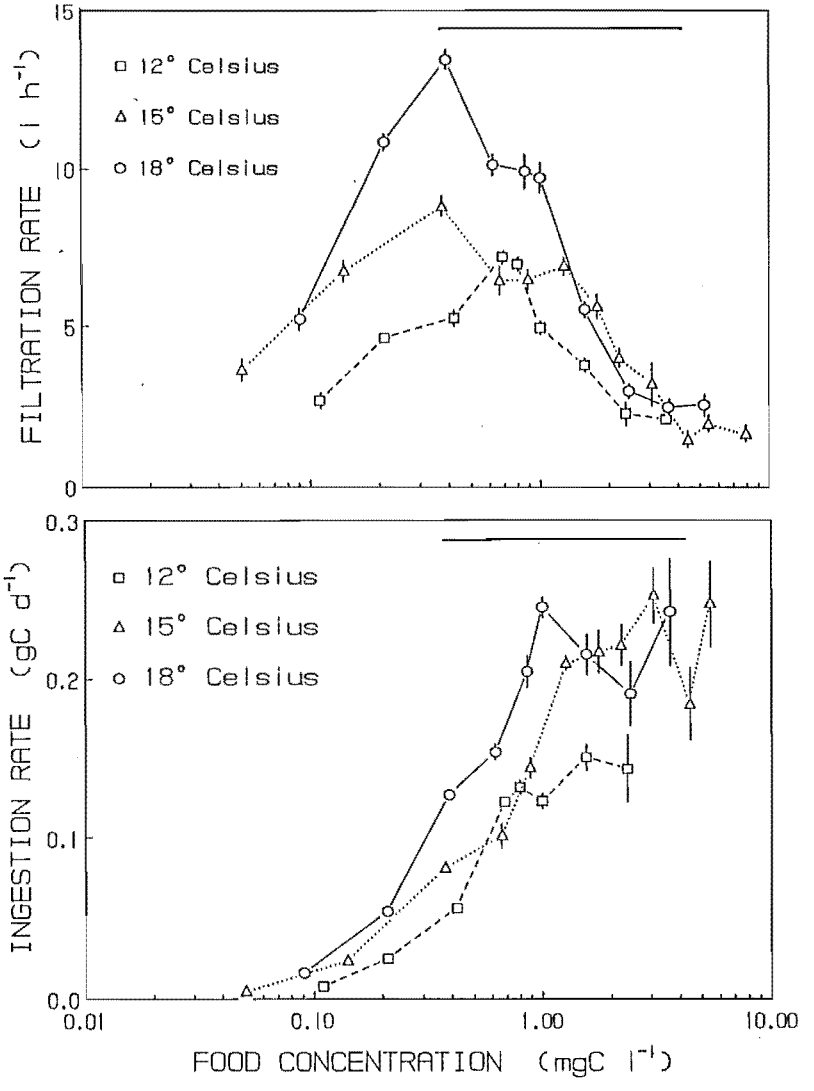

Figure 1. Above: Changes in filtration rate with temperature and food concentration.
Figure 2. Below: Changes in ingestion rate with temperature and food concentration. Horizontal bars show the range of food concentrations within mussel farms. Vertical bars show 95% confidence intervals.

higher food concentration than at either 15^{o} or 18^{o}C. At this temperature of 12^{o}C, filtration increased to a maxima of 7.2 l h^{-1} at 0.7 mgC l^{-1} food, but did not stabilise at intermediate food concentrations.

At maximum filtration rates, each mussel consumed 0.12, 0.08 and 0.13 gC d^{-1}, representing 91%, 36% and 57% of the maximum rations (below) recorded at temperatures of 12^{o}, 15^{o} and 18^{o}C, respectively (Figs 1 and 2). Mussels feeding at 12^{o}C therefore collected a substantially greater proportion of a maximal ration at maximum filtration rate than occurred at higher temperatures. However, the total volume ingested at maximal filtration rate were not markedly dissimilar at different temperatures, and some factor associated with ingestion rate may determine the concentration of food at

which maximal filtration occurs.

At all temperatures, filtration then decreased as food concentrations increased above 0.7, 1.4 and 0.8 mgC l^{-1} food, at which level maximal rations were first ingested by mussels maintained at 12, 15 and 18°C, respectively. This reduction in filtration maintained the ingestion of a constant, maximum ration as food concentration increased at each temperature (type 4 feeding, Section 3.2.1). Mussels consumed a maximum of 0.14, 0.23 and 0.22 gC d^{-1} at 12°, 15° and 18°C, respectively.

At most food concentrations, more water was filtered at higher temperatures. At 18°C, therefore, a similar, maximum ration was eaten at only 71% of the food concentration needed to collect a maximum ration at 15°C. However, the volume of food comprising this ration declined with temperature below 15°C, allowing mussels at 12°C to consume a maximum ration at only 60% of food concentrations required at 15°C. The lowest concentration at which maximum ingestion rates occurred were therefore temperature dependent and, during type 4 feeding, mussels obtained their maximum daily rations at food concentrations ranging from:

0.9-3.4 mgC l^{-1} (50,000-180,000 cells ml^{-1}) at 18°C,
1.4-4.4 mgC l^{-1} (75,000-242,000 cells ml^{-1}) at 15°C, and
0.8-2.4 mgC l^{-1} (45,000-131,000 cells ml^{-1}) at 12°C.

Pseudofaeces were produced at food concentrations exceeding 2.4-4.4 mgC l^{-1} (type 5 feeding) and, while marked production of pseudofaeces occurred, filtration rates were maintained at minimum rates of only 1.8-2.5 l h^{-1}. At these times more food was retained than had comprised this mussel's maximal ration during type 4 feeding. The incorporation of *I. galbana* into pseudofaeces prevented ingestion rate being determined from the rate at which *I. galbana* was removed from water. However, faeces were egested at similar rates during both feeding types 4 and 5. It therefore seems probable that maximum digestion rates were similar during both behaviours, and that only excess filtered food was ejected within pseudofaeces.

Gut Passage Time and Digestion

At temperatures of 12.5°, 14.8°, 16.5° and 18.9°C, half the radioactivity was defaecated in 290, 150, 120 and 125 minutes, respectively (Fig 3). GPT_{50} therefore increased exponentially as temperature decreased. A GPT_{50} curve was fitted using Maximum Likelihood fitting routines (Maximum Likelihood Programs, NAG), and the time taken to void 50% radio-activity at maximum ration was given by the equation:

$$GPT_{50} = 119 + (3136000 * 0.457^{T}) \qquad [r^2=0.99, \text{ F-test}, p<0.01]$$

where GPT_{50} is gut passage time (minutes) and T is Temperature (°C).

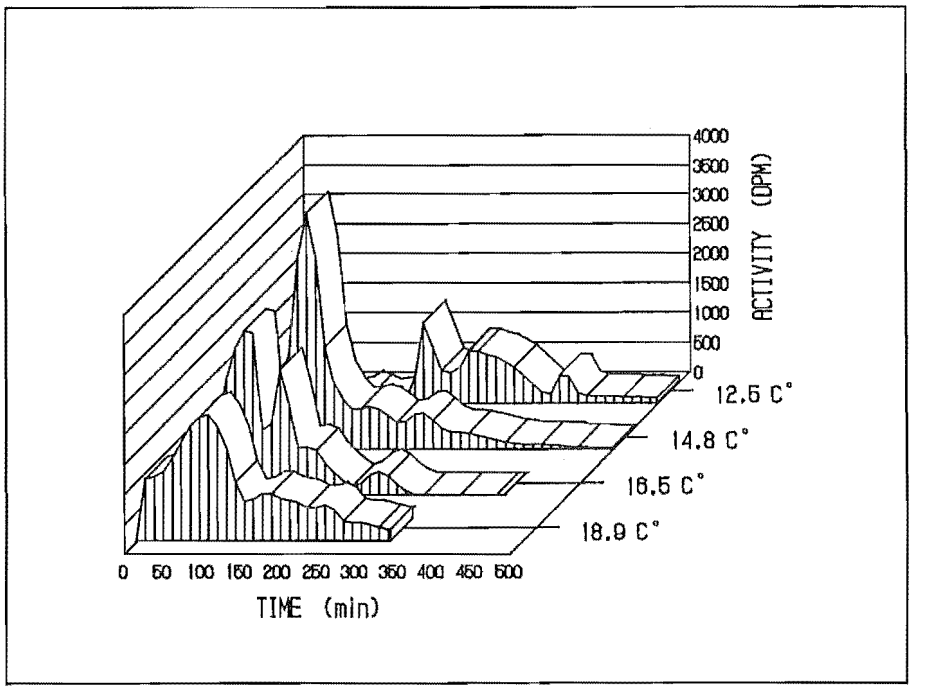

Figure 3. The influence of temperature on gut passage time.

It is hypothesised that the ingestion of a maximum ration was maintained by feedback from gut fullness receptors. If ration was limited by space available in the digestive tract, the mussels maximum ration would be inversely proportional to gut passage time at each temperature. Maximum ration therefore should decrease by 12% from 18^{o} to 15^{o}C, and by 47% from 15^{o} to 12^{o}C. In my experiments, however, maximum rations were similar at both 18^{o} and 15^{o}C, but declined 40% between 15^{o} and 12^{o}C. Nevertheless, regression analysis (MLP) showed the hypothesis explained 90% of the variance in maximum ration between temperatures ($p<0.01$), and it is likely that the volume of food ingested at high food concentrations is controlled through feedback from gut fullness receptors.

The composition of faecal particles varied with food concentration. At low ingestion rates (0.01 gC d^{-1}), few faeces were produced, they were thin in section, and tended to split along the anal groove. At intermediate ration levels (0.05-0.1 gC d^{-1}) however faeces were extruded more rapidly and were more cohesive, whereas at maximum ration (0.14-0.23 gC d^{-1}) large volumes of more friable faeces were produced. Whereas at high food concentrations *M. edulis* produced two discrete type of faeces having different carbon contents (Widdows et al 1979), *P. canaliculus* produced a single type of faeces which had uniform carbon content at different food concentrations.

Assimilation efficiency did not vary with ration within the range 0.01-0.23 gC d^{-1} *I. galbana* (Fig 4, ANOVA, $F=0.8$, $df=7$, $p=0.60$), nor did it vary with water

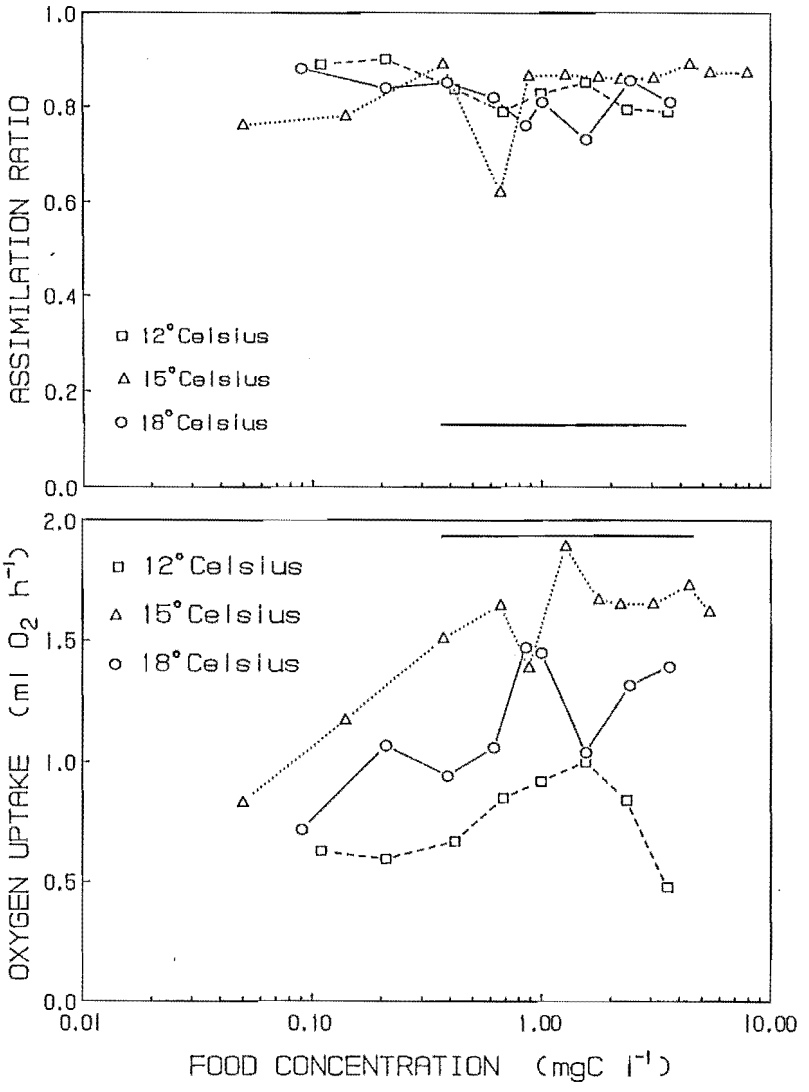

Figure 4 (above). Changes in assimilation efficiency with temperature and concentration of food. Horizontal bar shows food concentration within mussel farms.
Figure 5. Changes in oxygen uptake per mussel with temperature and food concentration. Horizontal bar shows food concentration in mussel farms.

temperature (ANOVA, $F=0.03$, $df=2$, $p=0.97$). Similar mean assimilation efficiencies of 82, 83 and 81% were determined at 18, 15 and 12°C, respectively. The volume of food ingested and digested, however, varied 50-fold with food concentration (ANOVA, $F=28.8$, $df=7$, $p<0.0001$) and also varied substantially with temperature (ANOVA, $F=18.7$, $df=2$, $p=0.0001$). Thus, the amount of food consumed by *P. canaliculus* was a major determinant of energy uptake. The factors (above) which determine ingestion rate and energy uptake probably exert pronounced effects on the biology of this mussel.

Respiration Rate

At each temperature studied, oxygen uptake increased as food concentration and the volume of food ingested increased ($r^2=0.69$-0.93, F-test, $p<0.02$, Table 1; Fig 5). As assimilation efficiency did not vary significantly with ingestion rate (see "Gut Passage

Time and Digestion" above), oxygen uptake was similarly correlated with carbon uptake from food.

In mussels consuming their maximum ration, oxygen uptake rates of 0.9, 1.7 and 1.3 ml O_2 ind^{-1} h^{-1} occurred at 12, 15 and 18°C in mussels of 2.2, 3.7 and 2.5 gDW, respectively. At 5% of maximum ration, oxygen uptake declined to 64%, 50% and 48% of the oxygen uptake recorded in mussels ingesting their maximum ration at these three temperatures. The intercepts of regression lines (Table 1) suggest that starved mussels took up 0.6 (12°), 1.0 (15°) and 0.7 (18°C) ml O_2 h^{-1}.

Weight specific oxygen uptake rates declined with temperature (ANOVA, $F=17.8$, $df=2$, $p=0.02$) and oxygen uptake was 0.42 (12°), 0.46 (15°) and 0.53 (18°C) ml O_2 g^{-1}DW h^{-1} in mussels ingesting a maximal ration. These relatively uniform weight specific rates of oxygen uptake suggested that the high body mass of mussels studied at 15°C probably affected their oxygen uptake. Indeed, regression analysis indicated that while changes in temperature explained only 15% of the variance in oxygen uptake by each mussel ($T=2.95$, $p=0.02$, delta $R^2=0.15$), changes in dry tissue weight probably explained some 86% of the variance in oxygen uptake ($T=-1.62$, $p=0.0001$, delta $R^2=0.86$). Thus, changes in body mass between mussels of similar length may be a key determinant of oxygen uptake, and condition index may, in part, determine the magnitude of aerobic respiratory losses.

TEMPERATURE (°C)	REGRESSION CONSTANT	REGRESSION COEFFICIENT	SIGNIFICANCE (F-test)	VARIANCE EXPLAINED
12	0.561	+0.112	<0.01	93%
15	1.052	+0.145	0.02	68%
18	0.720	+0.116	0.02	68%

Table 1. The regression of oxygen uptake (ml O_2 ind^{-1} h^{-1}) against ingested ration (10^8 cells h^{-1}) at 12°, 15° and 18°C.

Energy Transfer Processes

At all temperatures, mussels showed positive Growth Potential (GP) when provided with food (*I. galbana*) at concentrations greater than 10,000 cells ml^{-1} (0.18 mgC l^{-1}) (Fig 6). GP increased with ingestion rate, and was maximum at maximum ration; *cf* at >45,000, 75,000 and 50,000 cells ml^{-1}, at 12, 15 and 18°C.

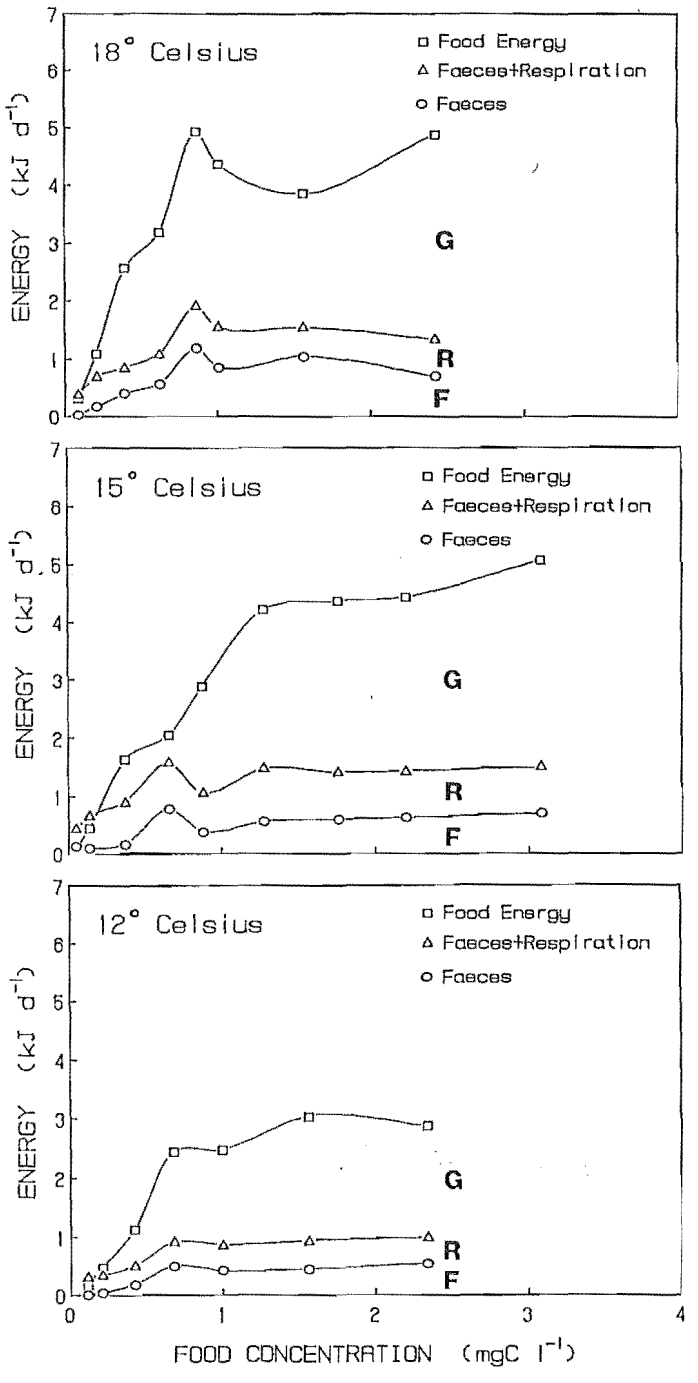

Figure 6. Effects of food availability and temperature on energy budgets (G:Growth Potential, R:respiration, F:faeces). Data is not corrected for changes in condition.

Table 2. Estimates of maximum Growth Potential (% body energy d^{-1}) in mussels of different condition, and at different temperatures.

WATER	DRY WEIGHT CONDITION INDEX		
TEMPERATURE	8% CI	10% CI	12% CI
12°C	3.97	2.98	2.31
15°C	5.42	4.09	3.25
18°C	5.11	3.85	3.16

While comparable estimates of GP were obtained within each group of mussels ingesting a maximum ration, GP varied notably between the three groups of mussels studied at different temperatures. GP was 1.4 times higher at 18°C (5.8% body C d^{-1}) than at 15° and 12°C (4.1% C d^{-1}, ANOVA, F=3.8, df=2, p=0.02).

Respirometry suggested that some variation in GP resulted from changes in body mass between groups. GP was therefore corrected for variation in condition index by dividing respiration losses by the ratio (standard condition index)/(actual condition index). The corrected respiration loss was then substituted into the energy budget equation (see Section 3.2.1, p.84). Three different standard condition indices of 8, 10 and 12% were used, a range which reflected the range of seasonal variation in the dry weight condition index of adult mussels of 80mm length (Section 2).

Corrected results (Table 2) indicated that GP was highest at 15°C, but a similar GP maxima occurred at temperatures of both 15 and 18°C. Metabolic rate declined with temperature so that the GP derived at maximal ingestion rate was 5% less at 18°C than at 15°C. Below 15°C, however, energy uptake decreased more rapidly with temperature than did metabolic rate, and at 12°C calculated GP was therefore 28% lower than in mussels feeding at 15°C.

Low condition enhanced corrected GP because respiration losses were reduced in mussels having a lower body mass (this study). Thus, mussels having an 8% condition index may grow 1.6 (18°C) to 1.7 (12°C) times more rapidly than those with a 12% condition index. Such changes in the condition of *P. canaliculus* may affect GP 1.7 times more severely than seasonal changes in temperature (Table 2), and condition is an important aspect to consider when discussing the principal causes of temporal variation in growth rate within natural mussel communities.

DISCUSSION

In *P. canaliculus*, temperature affected filtration rate, feeding behaviour, gut passage time, ration, oxygen uptake and growth potential. Sub-lethal temperatures are known to affect the nutrition and growth of other mussels (Gonzalez and Yevitch 1976; Incze et al. 1980; Sprung 1984a, b). Temperature may therefore be a key determinant of the flow of carbon through mussel communities. This present study indicated that variation in water temperature affected both the feeding behaviour and the critical food concentration thresholds at which changes in feeding behaviour occurred. This, in turn, determined the quantity of carbon assimilated from food, catabolism of energy containing compounds, and may eventually constrain the rates at which mussels increase in size, condition and reproductive potential.

Feeding Behaviour

In *P. canaliculus*, thresholds between different types of feeding occurred at different food concentrations in waters of different temperature. Such changes in dietary thresholds and feeding behaviour determined how much food was ingested at each food concentration. While important, these feeding patterns have been described and discussed in Section 3.2.1. This present discussion of filtratory behaviour is restricted to the different patterns of feeding recorded at different temperatures.

At 18°C, the five mode feeding behaviour of mussels of 80mm length resembled that described in Section 3.2.1 for mussels of 30, 60 and 80mm length maintained at 15°C. However, at 12°C types 2 and 3 of feeding behaviour did not occur, and gut passage time began to increase rapidly as temperature declined. It is therefore possible that basic changes in the physiology of these feeding processes occurred below this temperature.

Little comparative information is available on the feeding of other species of mussels. Only Walz (1978a) and Sprung (1984b) have studied filtration rate and food intake within a temperature-food concentration matrix, and over long periods (>4 h). Sprung found that filtration by larval *M. edulis* peaked at only 0.04-0.09 mgC l^{-1} *I. galbana*, and 9 of 13 curves that he presented showed filtration declined at food concentrations above this threshold as larvae ingested maximum ration. However, Sprung does not define discrete types of feeding behaviour and it is difficult to ascertain how feeding by adult *P. canaliculus* and larval *M. edulis* contrasted at low food concentrations. At higher food concentrations, however, both mussels showed similar tendencies to limit filtration and prevent ingestion rising in proportion to increasing food concentrations. In *M. edulis*, maximum ration increased rapidly to 12°C, then more gradually from 12-18°C. In *P. canaliculus*, maximal ration increased rapidly from 12° to 15°C, but was similar at 15° and 18°C. While each mussel may therefore be adapted to exploit different temperature ranges, the larval *M. edulis* studied by Sprung (above) were characterised by a different level of development to mature, adult *P. canaliculus* used during my study. Thus, it is interesting that mature freshwater mussels (*Dreissena polymorpha*) ingested their maximal ration at only 12°C (Walz 1978a), and also appeared adapted to feed most rapidly at lower temperatures than was *P. canaliculus*.

Interactions between filtration rate and maximum ration, two temperature dependent variables, determined the lowest food concentration that maximum ration was consumed at, at different temperatures. Maximum ration was 40% lower at 12°C than at 15°C, so this smaller ration was ingested at lower food concentrations and at lower filtration rates at 12°C. A similar maximal ration was ingested at both 15° and 18°C, and the higher filtration rates recorded at 18°C enabled maximum ration to be ingested at lower food concentrations at 18° than at 15°C. Ingestion may therefore

become limited by food concentration more frequently at temperatures approaching 15°C.

Food concentrations at which changes in feeding behaviour occurred appear to depend on food availability at low food concentrations, but become dependent upon interactions between filtratory and digestive physiology as food resources improve. An improved understanding of such relationships between feeding and digestive processes should be of value, but the regulatory mechanisms controlling observed transitions in feeding behaviour were seldom apparent during my study.

However, at food concentrations above 1 mgC l^{-1}, ingestion rate was correlated negatively with gut passage time, indicating that gut fullness could limit filtration rate. Thus, gut volume and rate of movement of food through the digestive tract may limit food intake and, ultimately, growth.

Gut passage time is a temperature dependent process (Garber 1983; Vahl 1979; this study) which regulates the ingestion rates of many invertebrates (Crisp and Southward 1961; Landry et al. 1984; Stemberger 1986) and fishes (Garber 1983; Vahl 1979; Windell and Bowen 1978). However, the rate of movement of food through the gut is not recognised as a factor affecting the feeding rates of mussels. Four points suggest that *P. canaliculus* regulated maximal ingestion through negative feedback from gut fullness receptors. [1] Filtration rate declined when digestive tracts became filled with food, 2-4 h after exposure to high food concentrations (Sections 3.1, 3.2.1). [2] Delays between changes in ingestion rate, and feedback which limits filtration last less than one gut passage time (Section 3.1). [3] Maximum ration increases in proportion to the cube of the mussel's length (Section 3.2.1). [4] The hypothesised inverse relationship between maximal ration and gut passage time was detected (this study). Thus, the maximum ration ingested during type 4 feeding was probably affected by the rate of transport of food past gut fullness receptors.

During type 5 feeding, food may be ejected in pseudofaeces because the digestive system of *M. edulis* cannot process more food (Widdows et al. 1979; Stromgren and Cary 1984). However, the production of pseudofaeces may also be a response to the respiratory demands of the mussel, and not simply a means of eliminating excess food. In *P. canaliculus*, oxygen uptake often declined while pseudofaeces were being produced (Section 3.2.1, this study), and during this time *P. canaliculus* also took up 60% of oxygen from water which had been cleared of food in transit across the gill. Thus, mussels may enter oxygen debt if filtration rate falls markedly below the low rates that were recorded while pseudofaeces were produced, and bivalves may regulate pumping rate in response to oxygen need (Epifanio et al. 1975) at high food concentrations. Conflict between the needs to respire or to conserve minor filtration costs could also explain why mussels filtered more rapidly than was needed to ingest their maximal ration, and why a

sub-optimal energetic strategy was employed during type 5 feeding.

Uptake of Carbon

Nutrient uptake by some mussels becomes limited by decreased digestive efficiency as the mussels ingestion rate increases (eg Thompson and Bayne 1974; Griffiths 1980). Nonetheless, my results indicate that digestive efficiency in *P. canaliculus* was not affected by either the ration ingested or changes in temperature.

Digestive efficiency may also vary between mussel species. At low food concentrations, *M. edulis* digested food only in the digestive gland and produced low carbon glandular faeces. At higher food concentrations, however, additional food was digested less efficiently in the gut and egested as intestinal faeces which contained more carbon (Widdows et al. 1979). In contrast, *P. canaliculus* did not produce two discrete types of faeces, and the fraction of carbon in faeces was similar at all food concentrations. This may be explained in three ways:

1) Extracellular digestive capacities of *M. edulis* (Widdows et al. 1979) were underestimated (see *Ostrea*: Mathers 1973),

2) Apparent differences between species were artifacts resulting from differences in experimental design (eg the duration of experiments and/or food quality), or,

3) Fundamental differences exist between species or populations of mussels.

From 74 to 83% of the carbon contained in *I. galbana*, used as food during my study, was shown to be taken up by both *P. canaliculus* and other bivalves (Gerdes 1983; Romberger and Epifanio 1981; this study). Because *I. galbana* is such a high quality food, digestive efficiency may not have declined at high ingestion rates.

Large rations of different algae are digested less efficiently by some other mussels. For example, assimilation efficiency of *M. edulis* declined from 76-33% as rations of *Phaeodactylum tricornutum* increased (Kiorboe et al. 1981; Mohlenberg and Kiorboe 1981; Widdows 1978a,b). Other algae (eg *Dunaliella* spp) were also digested less efficiently by *Aulacomya ater*, *Choromytilus meridionalis* and *M. chiliensis* as ingestion rate increased (eg Griffiths and King 1979; Griffiths 1980; Navarro and Winter 1982). If the ingestion of large quantities of food limits the proportion of food digested intracellularly, or the period that food is digested for, then the dependence of digestive efficiency on ration may reflect the lower digestibility of these algae relative to *I. galbana*. Energy uptake by *P. canaliculus* therefore may decrease if mussels ingest large quantities of less digestible foods. Digestion and carbon uptake by *P. canaliculus* may therefore be enhanced in hatchery systems and managed environments by providing high quality foods, and also be maximal in those natural environments dominated by easily digested phytoplankters such as the Marlborough Sounds (Section 2.2).

Oxygen Uptake

At all temperatures, oxygen uptake by *P. canaliculus* increased with carbon uptake. Further, estimates derived for starved mussels using regression analysis indicate that each mussel used from 48 to 64% less oxygen than the same mussel used after ingesting it's maximum ration. Oxygen uptake was also shown to decline with ingestion rate in bivalves (Bayne et al. 1976b; Widdows 1978b; Griffiths and King 1979; Navarro and Winter 1982) and other animals (Cladocera: Heisey and Porter 1977; Nematoda: Schiemer 1985). Reduction of aerobiosis may represent a widespread mechanism which allows animals to conserve energy while food is in short supply (Newell 1979).

Separate regression analyses also indicated that *P. canaliculus* having low condition respire less oxygen than mussels of high condition, resulting in the reduced expenditure of energy by mussels. Oxygen uptake declined when the condition of *M. edulis* declined after mussels had spawned (Widdows 1978a). During field studies on *M. edulis*, 58% of the variance in oxygen uptake could be attributed to a decrease in gonad index, while only 19% of the variance was attributed to seasonal successions in temperature (Bayne and Widdows 1978). These results are similar to those obtained for *P. canaliculus*, where oxygen uptake can decline five times more strongly due to changes in condition index ($R^2=0.86$, $p<0.0001$) than due to changes in temperature ($R^2=0.15$, $p=0.02$) occurring within ranges recorded in the field.

In several studies, oxygen uptake by mussels was found to increase as temperatures rose from 5 to 20^{o}C (Widdows 1973; Bayne and Widdows 1978; this study). During my field studies temperature ranged from 12-19^{o}C, and mussels both spawned and lost condition above 14^{o}C. As condition index was also correlated negatively with temperature (Section 2.2) it seems probable that, in mussels of similar size, the high weight-specific respiration rates which occurred at high temperatures were largely counterbalanced by the reduced aerobic respiration of *P. canaliculus* having low body mass (and condition index) during summer months.

The Energy Maximisation Hypothesis

Energy maximisation is a central tenet of optimal foraging theory (Taghon et al. 1978; Hughes 1980; Begon et al. 1987). While *P. canaliculus* is an efficient grazer, this study did not indicate that energy uptake was maximised.

Optimal foraging theorists predict that rapid filtration will begin when the net energy uptake exceeds the energy losses incurred during the capture and digestion of food (Hughes 1980; Lehman 1976). During type 1 feeding, however, *P. canaliculus* began rapid filtration after energy uptake exceeded total energy losses comprised by all factors. As filtration did not comprise a major cost, filtration effort was conserved at higher food concentrations than predicted for grazers maximising energy uptake.

During type 3 feeding, filtration rate was only 70% of the maximal recorded rate, yet these mussels did not ingest their maximal ration. Calculation indicates that up to 43% more food could have been ingested by mussels that filtered at their maximum rate, and it is apparent that energy uptake was not maximised.

Ration declined during type 4 feeding before digestive efficiency had declined, and this suggested that more carbon and energy could have been assimilated by mussels if they had ingested and digested a larger ration.

Discrepancies therefore exist between the energy maximization hypothesis of optimal foraging theory and the feeding behaviour of *P. canaliculus*, and other animals (Harper 1967; Carefoot 1973; Cook and Cockrell 1978). Such discrepancies probably result from the failure of the optimal forager theory to account for the inefficiencies of specific sensory capabilities which control feeding in different organisms (Inoye and Walker 1984; Begon et al. 1987), and for the delay between the availability of foods and the onset of dietary regulation (Section 3.2). Whereas dietary regulation may be based on nutrient uptake (Estabrook and Dunham 1976; Lehman 1976; Hughes 1980), volumetric control of diet also occurred in *P. canaliculus* and some fish (Vahl 1979; Windell 1978). The failure of the energy maximisation hypothesis to predict the feeding behaviour of the mussel suggests that optimal forager concepts should be applied to this animal with caution.

Growth Potential and Growth Efficiency

Variation in feeding thresholds and associated changes in Growth Potential (GP) are species specific phenomena which affect the vitality of an individual, and define an organisms niche (Schiemer 1985). The ecological relevance of experiments which define the niche is proportional to the degree of resemblance of experimental and natural systems. This study investigated material flow over ranges of temperature and food concentration occurring in Marlborough, and this system was typified by abundant food resources that were digested efficiently (Section 2.1). Results of experiments are therefore appropriate to the purpose in hand, but should be applied to divergent environments with caution.

A second limitation also restricts the application of the results. Energy requirements of mussels can be met by either aerobic or anaerobic metabolism. Below 5 ppm O_2, anaerobic metabolism contributed to the energy requirements of *M. edulis* (Famme et al. 1981). Anaerobic respiration was not measured in *P. canaliculus*, but at oxygen concentrations used in my study anaerobiosis contributed markedly less energy to *M. edulis* than aerobic metabolism. However, as the anaerobic losses of *P. canaliculus* were not determined, my calculations of GP only represent an upper potential for somatic growth plus reproduction.

P. canaliculus adjusted to food concentrations of 0.05-10.8 mgC l^{-1} in a complex manner. At all temperatures, GP either increased or was maintained as food concentration increased. However, GP declined at high food concentrations during some studies of other mussels (below), and the beneficial response of *P. canaliculus* to increased food could explain its rapid growth relative to other mussels (Flaws 1975; Hickman 1979). My research also suggested that experiment duration may induce variation in diet, digestion and growth between different studies (Section 3.2.1), and direct comparisons of various studies may prove to be misleading. I therefore only reiterate that this study determined material flow over 24 hours, and indicated that ingestion, energy uptake and growth potential did not decline at high food concentrations. This study therefore did not support the hypothesis that high food concentration inhibited growth.

Below food thresholds of 0.8-1.4 mgC, however, growth potential did become limited by the availability of food, and the impact that reduction of energy uptake probably had on growth may be estimated using a simple exponential model. On maximum ration, *P. canaliculus* could grow up to 4.1-5.2% body carbon d^{-1}, enabling body mass to increase approximately 10^6 times per annum. Mussels may, however, increase their weight by 1.8-3.4% C d^{-1}, and if mean growth rates fall below this range for protracted periods, they probably could not achieve this growth even if all carbon were used for to somatic development. Reduction in GP caused by changes in the food resource, mussel length or thermal variation can therefore become critical to both the growth and reproductive success of *P. canaliculus*.

While impacts of food concentration and mussel size on GP have been considered in several studies (see Section 3.2.1), few studies assess the impacts of seasonal changes in water temperature and food concentration on carbon flow. Sprung (1984a, 1985) has monitored the growth of mussels within a temperature-food concentration matrix, and under stable feeding conditions. Comparison of his study of larval *M. edulis* with my study of adult *P. canaliculus* is complicated by ontogenetic changes in physiology, and by temporal changes in mussel condition. Nevertheless, some common patterns did occur between the two studies, in both of which *I. galbana* was provided as food. Ingestion, growth rate and growth efficiency all reached maxima above food concentration thresholds, but these maxima occurred at lower food concentrations in larval *M. edulis* than in adult *P. canaliculus*. At high food concentrations, net growth efficiency was not markedly affected by temperature in either *M. edulis* or *P. canaliculus*, but the net growth efficiencies recorded for the two species did differ (*cf* 61-68% and 80-83%, respectively). Growth of *M. edulis* increased 1.5 times from 12 to 18°C whereas GP of *P. canaliculus* increased 1.3-1.4 times. At high food concentrations typical of mussel farming areas (>1 mgC l^{-1} food: Section 2.1), temperature may affect the growth of both

mussels more than food concentration, and temperature may be an important factor limiting growth of mussels in the field. However, in other situations somatic growth and reproduction may be more strongly dependent upon food availability (Barber et al 1987).

Mussel condition may also limit GP, and Table 2 indicates that increased condition reduced GP of *P. canaliculus* twice as strongly as seasonal changes in temperature. However, the impact of condition on growth was estimated by assuming all tissues respired at similar rates, whereas gonad, fatty tissues (*M. edulis*: Bayne and Scullard 1977) and glycogen storage tissues may have slower metabolic rates than other tissues. If this is true for *P. canaliculus*, then mussel condition may have less effect on GP than was estimated during my study.

Both high temperature ($>15^{o}C$) and low condition, two factors which enhanced growth potential, co-occur in summer, whereas during winter high condition and low temperatures predominated (Flaws 1975; Section 2.1) and GP can be expected to fall. Over an annual cycle, maximal GP may decline from a high of 5.1%, to a low of only 2.3% body C d^{-1} (Table 2).

M. edulis used 57% of its carbon uptake for gametogenesis (Rodhouse et al. 1985) and shed 74% of it's organic matter during spawning (Perez and Roman 1979). *P. canaliculus* also shed 51% of it's body mass while spawning, and this negative somatic growth which occurred in *P. canaliculus* during summer (Section 2.1) suggests that the additional energy available for growth during summer was probably ejected as gametes. Temperatures below $15^{o}C$ may suppress oogenesis (Maung Myint and Tyler 1982), and make greater proportions of the GP available for somatic growth. Note, however, that natural communities must reproduce to survive whereas the success of cultivated communities is measured by somatic production. Therefore, different optimal thermal and nutritive regimes exist for natural and commercial bivalve communities.

Variation in the size of the maximum ration of *P. canaliculus* caused marked variations in carbon uptake and Growth Potential between 12^{o} and $18^{o}C$, and the reduction of temperature from 15^{o} to $12^{o}C$ caused a 2.8-fold decline in maximum ration and carbon uptake. Extension of the gut passage time equation beyond the range of observations also suggested that ingestion may decline 7.6 times between 12^{o} and $9^{o}C$. While moderate reductions in temperature to $12^{o}C$ may suppress oogenesis and promote somatic growth, temperatures below $12^{o}C$ are therefore probably detrimental to the growth of this mussel stock.

Complex changes in Growth Potential and resource allocation can therefore occur between similar mussel communities living in food rich waters, as a result of changes in temperature. Seasonal and geographic variation in food concentration recorded in Marlborough also limited feeding and growth within the temperature range tested

(Section 2). Spatial and temporal changes in temperature and food availability therefore cause marked spatio-temporal variation in the growth potential of *P. canaliculus* over the ranges of both factors studied. Latitude, location, and season are therefore key elements associated with changes in production within, and also between different mussel communities.

SECTION 4.

Synthesis

The scientific objectives of this investigation were:

1) To identify locations where environmental factors may limit feeding and growth,

2) To define a range of factors limiting food uptake at different spatial scales,

3) To determine the mussel's feeding response to variation in each factor, and

4) To understand how mussels may feed over greater ranges of environment than occurred in Marlborough, and so attempt to predict growth in other systems.

This concluding discussion assesses the extent to which these objectives have been met during the present study and then relates some implications of my research to the future development of the mussel cultivation industry.

Whereas the first and second objective were achieved to a substantial degree, and discussed in Section 2, subsequent objectives were pursued in separate parts of this thesis. Results have not therefore been developed as an integrated model of feeding by *P. canaliculus* in response to environmental change. Conceptual ~~modeling~~ modelling is one method of ordering observations pertaining to complex situations (Lauder 1987). A conceptual model of feeding and related responses of *P. canaliculus* to transitions occurring within its environment will now be developed. During the development and application of this model, the second, third and fourth objectives will also be discussed.

Feeding rates and food dependent processes play an important role in determining interactions between grazers and their habitats. Eight variables are now known to influence the feeding of *P. canaliculus*, and probably interact to determine feeding by mussels in both natural and farm environments.

The nutritional status of the mussel has been shown to be dependent upon food concentration, fractions of refractory matter within the diet, the mussel's length, and temperature. Whereas these variables determined feeding at most times, low salinity and oxygen concentration, spawning, and food resource instability may also limit food uptake intermittently. The concurrence of slow current speed and high stock density also accentuated the depletion of food resources within the mussel farm and indirectly reduced the mussel's ration. These factors comprised the major factors that controlled feeding and nutrition of *P. canaliculus* within intensive mariculture systems (Section 2).

Having denoted factors that determined feeding rate, the response of mussels to such factors needs to be established. Feeding by mussels in the laboratory (Section 3)

can indicate how environmental change was tolerated, and the feeding curves obtained during experimental studies describe the mussel's feeding behaviour in response to variation in factors identified as determinants of food intake during Section 2 (third objective). Indeed, the only factor that statistical analysis indicated as a control of gut content which was not studied in experimental situations was the role of PIM in determining diet and energy uptake. Experimental information is also useful in predicting situations in which *P. canaliculus* can feed well, and should develop most rapidly, but which I may not have recorded in mariculture systems. In Marlborough, food concentration varied from 0.3 to 4.0 mgC l^{-1}, salinity was typically above 30ppt and oxygen tension approached saturation. The laboratory studies summarised below also enhance our understanding of how mussels may feed and grow over a greater range of conditions than were sampled in mussel cultures (fourth objective).

At food concentrations below 0.1 mgC l^{-1} negative Growth Potential was recorded, and it is unlikely that *P. canaliculus* would survive protracted exposure to less food. Growth increased with food concentration to maximal values at 1 mgC l^{-1} food, and rapid growth may occur from 1 to 10 mgC l^{-1} (Sections 2.1, 3.3).

The rate of change in food concentration also affected feeding, and could limit growth of mussels. Feeding adapted to marked change in food concentration over 6-16 hours (Section 3.2), however, and such extreme and rapid changes in food concentration may not occur in Marlborough (Section 2.1). Instability of food resources may therefore affect feeding infrequently in some ecosystems.

Whereas feeding and Growth Potential was maximal at temperatures of 15-18^{o}C (Section 3.3.2), low temperature may enhance the condition of mussels in the field. However, rates at which mussels increased in length were similar from 12 to 18^{o}C (Section 2). Thus, the optimal temperature range for shell growth may exceed 12-18^{o}C, whereas condition index may be enhanced at temperatures below 15^{o}C. Nonetheless, rapid feeding and marked growth of mussels occurred at all temperatures recorded within the Marlborough Sounds.

Sudden reduction of salinity from 34ppt to 25ppt induced temporary cessation of feeding, but mussels fed rapidly only 8 hours after such a marked change in salinity (Section 3.2). Feeding adapted to a range of salinity in excess of that normally recorded in Marlborough, and mussels may grow rapidly within this range of stable, saline environments.

Oxygen concentration did not limit filtration rate within the range 5-7 ppm (Section 3.2) and, as oxygen varied within this range in mussel farms, probably did not affect feeding in Marlborough. However, filtration declined 10-fold as oxygen declined from 5.0 to 1.5ppm. Below 5ppm O_2, low oxygen tension may limit feeding by mussels.

Presence of gametes was also associated with lower feeding rates (Section 3.1),

but food resources sampled within mussel farms indicated that gametes were either produced intermittently, or settled rapidly and did not constrain feeding for protracted periods. Presence of gametes may, however, limit feeding within some natural and benthic communities.

Both field and experimental studies have determined that mussel size, temperature and food concentration are key determinants of feeding behaviour and food intake by *P. canaliculus*. In addition to the responses recorded within mariculture systems, laboratory studies indicated that the presence of gametes, oxygen tension, salinity and feeding history were partial determinants of food uptake by mussels. The present studies have therefore contributed to our understanding of how different factors affect the feeding of mussels, and how such factors affect diet under some conditions not recorded in the field.

A range of conditions under which *P. canaliculus* feeds adequately has also been defined, and the minimum requirements of an optimal culture regime for *P. canaliculus* were found to be stable concentrations of 1-10 mgC l^{-1} food (<4 mgC l^{-1} being favoured), temperatures of 12-18^{o}C, salinities of 25-34ppt (34ppt being favoured), oxygen concentrations of 5-7ppm, an absence of gametes, and the regular or continuous replenishment of algal culture and seawater. This regime was largely defined using adult mussels of 60-100mm length, and may be less suited to the biological needs of larval and juvenile stocks. Nevertheless, this regime can be expected to support rapid development of mussel stocks of different length classes, and also represents a suitable regime for conditioning adult mussels under hatchery conditions.

Information describing changes in feeding in response to environmental variation is also useful in defining critical values of different parameters that regulate the feeding of *P. canaliculus* within a model (Fig 1). As most factors affecting feeding showed marked changes during field studies, conceptual models of nutrition in *P. canaliculus* need to emphasise the dynamic nature of nutritive processes in both space and time. Key components of this model include the primary determinants of energy uptake (food concentration, digestibility of food and presence of dietary silt), and two secondary factors affecting ingestion rates (water temperature and mussel length). On some occasions the net effect of these factors can also be attenuated by other factors (eg oxygen concentration, salinity, presence of gametes, and stability of food resources). These attributes interact to regulate the diet and energy uptake of *P. canaliculus*, and therefore may determine the growth and development of the mussel at different sites.

Comparison of the field environment with laboratory data indicated that feeding behaviour within mariculture systems was less complex and more stable than a cursory examination of this model would suggest. In Marlborough, magnitudes of changes in

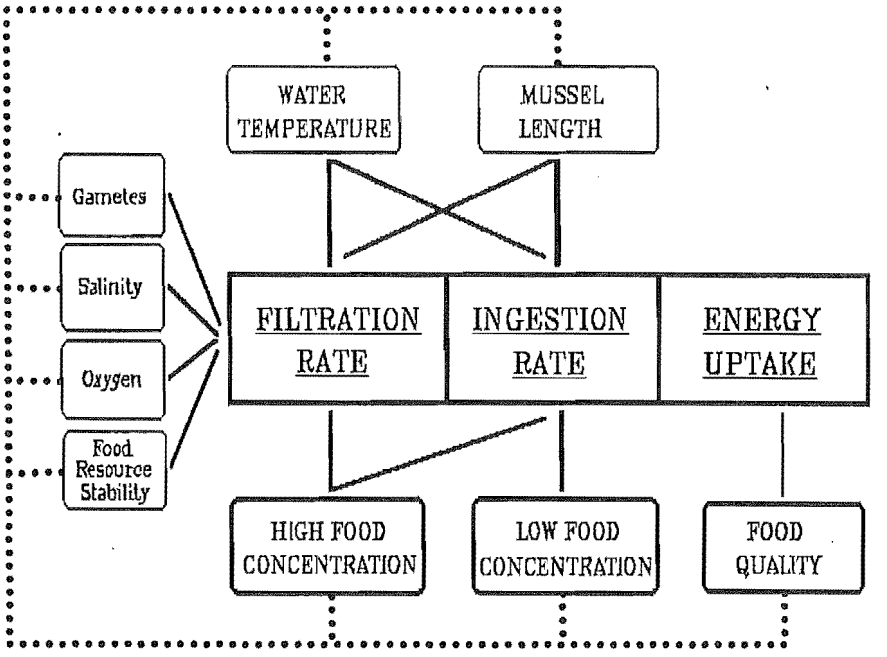

Figure 1. A conceptual model of feeding by the mussel.

oxygen concentration and salinity are unlikely to affect feeding markedly, and gametes were not found within mussel farms. Food concentrations were also relatively stable over a 12 hour period (Hickman et al. in prep), and seasonal, thermal successions and mussel size probably only affect the mussel's feeding markedly over protracted time periods. Thus, whereas changes in water temperature and mussel size induced marked but slow successions of food intake and energy uptake, dynamic attributes such as food concentration and food quality are probably the most important variables inducing spatial variation of diet and realised growth of *P. canaliculus* within the Marlborough Sounds (see second objective).

The feeding behaviour of *P. canaliculus* derived using multivariate analyses of field data appeared to be consistent with that determined within the laboratory. Mussel feeding was not markedly affected by salinity changes within the normal environmental range of 30-34ppt, or following reduction of salinity from 25 to 34ppt in the laboratory (Section 3.2). Whereas oxygen concentration was shown to inhibit filtration below 4 ppm O_2 in laboratory trials, oxygen did not affect feeding at higher oxygen concentrations in the field. Mussel length was also a major determinant of filtration rate, diet and energy uptake at all food concentrations, and within both studies. Regression analysis indicated seasonal changes in temperature caused filtration by mussels of 80mm length to increase by 9 l h^{-1} in the field, and this rate increased by 6 l h^{-1} in the laboratory as temperature increased from 12 to 18°C. Temperature was also identified as an important factor affecting feeding during both field and laboratory research

programmes.

However, the structure of the food resource was probably the single most important factor limiting the growth and development of the mussel. Statistical analysis showed that two dominant types of feeding behavior occurred between 0.4 and 4 ug l^{-1} chlorophyll *a* in the field; production of pseudofaeces also indicated that an additional feeding behaviour occurred at high food concentrations in the field (unreported data). In the laboratory, types three and four of filtration occurred over this range of food concentrations, and type five feeding also occurred above thresholds of 2.4-4.4 mgC l^{-1} (*cf* 2.7-4.9 ug chlorophyll *a*). Both field and laboratory studies therefore identified three analogous modes of feeding which occurred over similar ranges of food concentration.

Water temperature, food concentration and mussel size were major controls of the filtration and ingestion rates of *P. canaliculus* in both the laboratory and the field. Food concentration limited the nutrition of mussels in the outer regions of the Marlborough Sounds, and reduced both the diet and development of mussels within farms. However, other factors seldom inhibited feeding rates within the area, and this absence of persistent limitation of feeding rate may contribute both to the rapid growth (Flaws 1976; Hickman 1979; this study) and high condition (Hickman and Illingworth 1980; this study) of *P. canaliculus* in Marlborough.

Seed (1976) states that presence of "adequate food" is a requisite for growth, regardless of all other factors. This concept was supported by the results of my study. However, concepts of adequate food must encompass the different digestibility and availability components.

The dietary threshold at which a maximal ration is first ingested may be the lowest food concentration at which maximum growth occurs, and could represent the lowest concentration of food that can be used within a growth system optimised for *P. canaliculus*. Both field and laboratory studies indicated that this threshold feeding occurred, and that energy uptake was no longer food limited above this threshold of satiation. Whereas feeding was food limited below 0.8-1.4 mgC l^{-1} during laboratory studies (Section 3.3), field work indicated that feeding probably became limited below higher thresholds of 1.4-1.7 mgC l^{-1} food (Section 2.2). However, mussels depleted water next to culture ropes of food (Section 2), and more concentrated food was sampled than was filtered by mussels. Thus, these ranges were not dissimilar, and higher thresholds indicated by results of field studies can be explained by the depletion of food.

Silt can comprise a major fraction of refractory matter present in turbid seawater, and ingestion of silt can reduce diet quality (Theisen 1977; Bricelj and Malouf 1984; Bricelj et al 1984; Robinson et al 1984; Bayne et al. 1987). Whereas *P. canaliculus* ingested maximal food above 1 mgC l^{-1}, refractory matter displaced digestible foods

from the diet at high food concentrations. At high food concentrations, the relative abundance of silt was also associated with reduced condition of mussels (Section 2.2), supporting the hypothesis that ingestion of indigestible matter had reduced energy uptake at high food concentrations. However, whereas phytoplankton quality did not appear to constrain growth in Marlborough, this factor may be important in places other than Marlborough.

Implications to the Industry

Mussel farm communities have a high biomass and biological activity which indicated that cultivated *P. canaliculus* is a key element of Marlborough ecosystems (Brinkhurst 1974). Thus, the presence of this mussel may exert marked influences on dependent organisms, and features affected by the mussels feeding (such as food depletion) probably exert pronounced influences within mussel farm communities.

During my investigations, food availability was shown to exert pronounced effects on both the feeding and production of mussels both between different farms located in different embayments, and within the farm. Such variation did not occur between farms in Crail Bay, but this assessment is only valid for the specific pattern of farm distribution studied within Crail Bay. The effects of modifications to the present stock distribution now need to be determined.

Feeding rates recorded during the present study can only be used to estimate impacts that farmed mussels had on the food resources occurring within specific mussel farms, and in surrounding waters. Nonetheless, calculations based on the data collected showed two interesting interactions occurring within and between mussel farms.

Firstly, feeding can be compared to the influx of food into a farm. Some 3.5 x 10^6 mussels lived in one moderately stocked farm in Crail Bay, and estimates suggest that each mussel of 80mm length filtered up to 13.4 l h^{-1} water of food. This community filtered up to 50,000 tonnes water per hour of the 35-103 x 10^3 tonnes h^{-1} which flowed through the farm and removed up to 60% of the food from seawater (Section 2). This is not inconsistent with estimates (above) that 0.7 to 2.1 tonnes of seawater flowed through the farm for each tonne of water filtered by mussels.

Secondly, the area required to support maximal growth in one heavily stocked mussel farm can be estimated. Mackenzie et al. (1986) determined gross primary production in Kenepuru Sound as 0.57 gC m^{-2} d^{-1} in bright summer light. During summer, each mussel of 80mm length consumed 0.22 gC d^{-1} (Section 3), or the primary production from an area of 0.4 m^2. Thus, the 5.5 x 10^6 mussels living in the farm at Schnapper Point (Kenepuru Sound) probably cleared primary produce from an area of 2.1 Km^2, or an area 200 times that occupied by the farm. As little as 0.5% of the carbon consumed may therefore be produced within that marine farm at Schnapper Point.

This is important as it was shown in Section 2.1 that nutritional interference did not occur between adjacent mussel farms at their present separation. However, the calculation indicates that each mussel farm is dependent on the import of food. Thus, the question of whether farms interfered with each other within embayments becomes the question " How many farms can coexist before marked nutritional interference does occur ? " Risk is created by establishing further farms without adequate monitoring of the biological consequences of any management decisions which increase the density of stock. Such monitoring is not conducted at present.

Adequate transport of externally produced food is needed to supply food to farmed mussels. Without adequate flow, farms can deplete food from substantial areas of the Sounds and reduce the concentration of phytoplankton available to other grazers. Redesign of mussel farms to reduce both the attenuation of currents and the depletion of food should also enhance the growth of mussels and protect the habitats of the other grazers. Good management of mussel farms and the effective conservation of the ecosystem, therefore, are not necessarily exclusive goals.

Management may affect the productivity of mussel farms by:

[1] Appropriate selection of sites to be farmed,

[2] Appropriate design and emplacement of initial farm structures, and

[3] Through testing and subsequent modification of farm structures.

Identification of superior areas for mariculture, and the determination of an appropriate distribution of farms in each culture area may enhance the viability of each newly developed farm. Some natural constraints on feeding and growth were identified in this thesis (above), and that information should be used in for the selection and development of farm sites.

Both the distribution and internal structure of mussel farms appear to impose major limitations on the nutrition and growth of mussels within the longline culture systems studied. It was noted that the factors classifying condition index using discriminant analysis were: (1) water temperature, (2) shell length, (3) volumes of water cleared of food, and also (4) crowding by adjacent mussels (Section 2.2). Additional food factors may also limit condition index (PIM and chlorophyll concentrations: Regression analysis, Section 2.2). These observations are interesting because three dietary factors were implicated as determinants of condition index, and three other factors (mussel length, crowding and water temperature) are also known to affect community filtration rates and so food depletion within the mussel farm. Management of mussel farms to reduce the negative impacts of food resource depletion may therefore enhance both the mass and quality of mussels present at harvest.

All of the above factors can be managed either through administration of the Marine Farming Act (1971) or by manipulating farm structures.

The Marine Farming Act gives authority to the Crown to restrict development of mussel farming to those regions that are most suited to this form of aquaculture. Having been granted a Marine Farming Permit, mussel farmers are then free to develop stocking patterns that optimise growth within constraints imposed by environmental factors operating within their situation. My analysis indicates that research directed to developing appropriate site selection and farm management criteria can both improve the condition of mussels at harvest, and enhance product quality within the industry. However, such criteria have not been adequately defined at present.

Feeding and growth of mussels living in farm communities is viewed as a particular, complex scaling problem about which inadequate information exists. Continued research on the environmental limits to growth operating at each spatial scale should encourage the establishment of improved management practices (at both government and industry levels), and result in the enhancement of productivity and profitability throughout the mariculture industry.

Research and development work must be targeted not only to identify, but also to manipulate those physico-chemical and nutritional factors affecting meat yield at different scales. When manipulation is not practicable, then benefits accrued through research are substantially reduced. Such research should identify embayments which support the rapid growth and high condition of mussels so that their future development can be determined. In addition, locations that are most suitable for the future development of mussel culture systems must be identified so that mariculture units are distributed over a more extensive geographic range of sites. Most importantly, management strategies must be developed that allow farmers to optimise the growth and condition of mussels within extant mariculture systems. Continued research on the functional morphology of individual farms needs to become a research priority because manipulation is most possible at this level of organisation.

While transplantation trials (see Section 2.1) provide one means of evaluating different sites, more detailed and fundamental research must be conducted. The efficient exploitation of existing foods has been discussed, but it should be stressed that variable interactions between the production, transport and consumption of food will determine the biomass of mussels that can be sustained within a region, embayment or mussel farm. Thus, maximal stock levels are dependent on inadequately defined phenomena such as the biomass and productivity of phytoplankton, hydrodynamic attributes of farmed areas, and reduction of food due to grazing by the mussels present. There is therefore a special need for continued research into:

[1] The kinetics of water and food movement within embayments and farms,

[2] The production and biomasses of phytoplankton and additional foods,

[3] The engineering of improved farm structures to promote flow, and,

[4] Interactions between the form and biological function of mussel farms.

These projects require expertise outside the traditional skills of many fisheries biologists, yet require understanding of the nutritive biology of the mussel to generate useful information. I suggest that subsequent research would be most efficiently conducted by an interdisciplinary team pursuing an objective of understanding, rather than merely describing the system.

The consistent occurrence of "adequate food" is probably the single most important factor determining the suitability of the Marlborough area for mussel culture. Food resources varied between embayments and within mussel farms, and overstocking could induce additional variation within a bay. Results of food resource assays cannot therefore be applied outside the region sampled. Such analysis is also costly, and the expense may not be justifiable for data of limited application. It is not currently feasible to predict the mussel's growth or condition on the basis of food concentration alone. Thus, direct measurements of condition in transplanted mussels may provide more useful, short-term indicators of the biological status of a mussel resource, than assays of food alone.

Both government and individual farmers need to ensure that neither the growth or condition of farmed mussels is allowed to become limited by any reduction of food concentrations within cultivated embayments, or in individual farms. Transplantation of stock, and comparisons of condition and growth between locations (Section 2.1) appear to provide a cost-effective method of assessing whether growth has become limited by the availability of food. Such methods should become standard procedures used to compare different locations. Although this may enhance efficiency within the industry, the ultimate objective of maximising productivity and profit is likely to be achieved only through continued research and development effort.

Future development of the mariculture industry is therefore dependent on the funding provided by both government and industry for specific research programmes targeted to understanding how management affects production. At the conclusion of this study neither party funds or conducts field research in Marlborough. As both parties benefit from improved meat yield through earnings generated by commerce, taxation and export, each party should review their attitude and commitment to ongoing research into the biological bases of mussel productivity.

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"I is a very mixed up Giant", the Giant said. "But I does do my best. And I is not nearly as mixed up as the other Giants. I know one who gallops all the way to Wellington for his supper."

"Wellington?" Sophie said. "Where is Wellington?"

"Your head is full of squashed flies," the Giant said. "Wellington is in New Zealand. The human beans in Wellington has an especially scrumdiddlyumptious taste, so says the Welly-eating giant."

"What do the people of Wellington taste of?" Sophie asked.

"Boots," the Giant said.

"Of course," Sophie said. "I should have known."

And for his invaluable advice which I have endeavoured to follow:

"Don't gobblefunk around with words."

Literature Cited

Baars M.A. and Helling G.R. (1985) Methodological problems in the measurement of phytoplankton ingestion rate by gut fluorescence. Hydrobiol. Bull. *19*, 81-88.

Barber B.J.; Getchell R.; Shumway S. and Schick D. (1988) Reduced fecundity in a population of the giant scallop *Placopecten magellanicus* in the Gulf of Maine, U.S.A. Mar. Ecol. Prog. Ser. *42*, 207-212.

Bayne B.L. (1976) Marine mussels: their ecology and physiology. Cambridge University Press, London. 410 pp.

Bayne B.L.; Widdows J. and Newell R.I.E. (1976) Phyiological measurements on estuarine bivalve molluscs in the field. Pp 57-86 in Proc. 11th European symposium on marine biology. Keegan B.; Ceidigh P. and Boaden P. (eds.). Galway, 1976.

Bayne B.L. and Scullard C. (1977) Rates of nitrogen excretion by species of *Mytilus* (Bivalvia: Mollusca). J. Mar. Biol. Ass. U.K. *57*, 355-369.

Bayne B.L. and Widdows J. (1978) The physiological ecology of two populations of *Mytilus edulis* L. Oecologia (Berl.) *37*, 137-163.

Bayne B.L. and Worral C.M. (1980) Growth and production of mussels *Mytilus edulis* from two populations. Mar. Ecol. Prog. Ser. *3*, 317-328.

Bayne B.L.; Hawkins A.J.S. and Navarro E. (1987) Feeding and digestion by the mussel *Mytilus edulis* L. (Bivalvia: Mollusca) in mixtures of silt and algal cells at low concentrations. J. Exp. Mar. Biol. Ecol. *111*, 1-22.

Begon M.; Harper J.L. and Townsend C.R. (1987) Ecology: individuals, populations and communities. Blackwell Scientific, London.

Beklemishev C.W. (1961) The influence of the atmospheric cyclones on the whale feeding grounds in the Antarctic. Akad. Nauk SSSR, Inst. Okeanol., Trudy *51*, 121-141.

Beukema J.J.; Cadee G.C. and Jansen J.J.M. (1976) Variability of growth rate of *Macoma balthica* in the Wadden Sea in relation to the availability of food. Pp 69-78 *in* Proc. 11th European symposium on marine biology. Keegan B.; Ceidigh P. and Boaden P. (eds.). Galway, 1976.

Bjorndal K.A. (1985) Use of ash as an indigestible dietary marker. Bull. Mar. Sci. *36*, 224-230.

Blake N.J. and Sastry A.N. (1978) Neurosecretory regulation of oogenesis in the bay scallop *Argopecten irradians irradians* (Lamark). Pp 181-190 *in* Proc. 13th European biology symposium. Permagon Press, Oxford.

Borrero F.J. and Hilbish T.J. (1988) Temporal variation in shell and soft tissue growth of the mussel *Geukensia demissa*. Mar. Ecol. Prog. Ser. *42*, 9-15.

Bowman M.J.; Esaias W.E. and Schnitzer M. (1981) Tidal strirring and the distribution of phytoplankton in Long Island and Block Island Sounds. J. Mar. Res. *39*, 587-603.

Bradford J.M.; Lapennas P.; Murtaugh R.; Chang F. and Wilkinson V. (1986) Factors controlling summer phytoplankton production in greater Cook Strait, New Zealand. N.Z. J. Mar. Freshwat. Res. *20*, 253-279.

Bradford J.M. and Chang F.H. (1987) Standing stocks and productivity of phytoplankton off Westland, New Zealand, February 1982. N.Z. J. Mar. Freshwat. Res. *21*, 71-90.

Bradford J.M.; Chang F.H.; Baldwin R.; Chapman B.; Downes M. and Woods P. (1987) Hydrology, plankton, and nutrients in Pelorus Sound, New Zealand, July 1981 and May 1982. N.Z. J. Mar. Freshwat. Res. *21*, 223-233.

Bricelj V.M. and Malouf R.E. (1984) Influence of algal and suspended sediment concentrations on the feeding physiology of the hard clam *Mercenaria mercenaria*. Mar. Biol. *84*, 155-165.

Bricelj V.M.; Malouf R.E. and Quillfeldt C. (1984) Growth of juvenile *Mercenaria mercenaria* and the effects of resuspended bottom sediments. Mar. Biol. *84*, 167-173.

Bricelj V.M.; Epp J. and Malouf R.E. (1987) Comparative phsiology of young and old cohorts of bay scallop Argopecten irradians irradians (Lamark): mortality, growth and oxygen consumption. J. Exp. Mar. Biol. Ecol. *112*, 73-91.

Brinkhurst R.O. (1974) The benthos of lakes. MacMillan, London. 190 p.

Buss L.W. (1981) Planktonic food availability and suspension feeder abundance: evidence of in situ depletion. J. Exp. Mar. Biol. Ecol. *49*, 151-161.

Cabanas J.M.; Gonzalez J.J. and Marino J. (1979) A study of the mussel and its epifauna in the floating mussel farms of the Arosa Estuary. III. Preliminary observations concerning particle retention and biodeposition in one mussel raft. Bol. Inst. Espa. Oceano. *V*, 45-50.

Calow P. and Fletcher C.R. (1972) A new radiotracer technique involving 14-Carbon and 51-Cromium for estimating the assimilation efficiencies of aquatic primary consumers. Oecologia (Berl.) *9*, 155-170.

Carefoot T.H. (1973) Feeding, food preference and uptake of food energy by the supralittoral isopod *Ligia pallasii*. Mar. Biol. *18*, 228-236.

Chanley M.H. (1981) Laboratory culture of marine bivalve molluscs. Pp 233-249 *in* Marine invertebrates as laboratory animals. National Academy Press, Washington.

Chantry M.; Dugas R.J. and Eastly K.A. (1983) Optimum salinity regime for oyster production on Louisiana's state seed grounds. Contributions in Marine Science *26*, 81-94.

Chatterji A.; Ansari Z.A.; Ingole B.S. and Parulekar A.H. (1984) Growth of the green mussel, *Perna viridis* L., in a sea water recirculating system. Aquaculture *40*, 47-55.

Conover R.J. (1966) Assimilation of organic matter by zooplankton. Limnol. Oceanogr. *11*, 338-354.

Conover R.J.; Durvasula R.; Roy S. and Wang R. 1986 Probable loss of chlorophyll-derived pigments during passage through the gut of zooplankton, and some of the consequences. Limnol. Oceanogr. *31*, 878-887.

Cook R.M. and Cockrell B.J. (1978) Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. J. Anim. Ecol. *47*, 529-547.

Crisp D.J. (1984) Energy flow measurements. Pp 245-283 *in* Methods for the study of marine benthos (2^{nd} edition). Holme N.A. and McIntyre A.D.(eds.). Blackwell Scientific, Oxford. 387 pp.

Crisp D.J. and Southward A.J. (1961) Different types of cirral activity of barnacles. Phil. Trans. Roy. Soc. (Lond.) Ser. B *243*, 271-307.

Dagg M.J. (1976) Complete carbon and nitrogen budgets for the carnivorous amphipod *Calliopius laeviusculus* (Kroyer). Int. Revue der Gesamten. Hydrobiol. *61*, 297-357.

Dame R.; Zingmark R. and Stevenson H. (1980) Filter feeder coupling between the estuarine water column and benthic subsystems. Pp 521-526 *in* Estuarine Perspectives. Kennedy V.S.(ed). Academic Press, London.

Davis J.A. (1986) Boundary layers, flow microenvironments and stream benthos. Pp 293-312 *in* Limnology in Australia. DeDecker P. and Williams W.D. (eds.). Junk, Dordrecht.

Downs J.N. and Lorenzen C.J. (1985) Carbon:phaeopigment ratios of zooplankton fecal pellets as an index of herbivorous feeding. Limnol Oceanogr *30*, 1024-1036.

Duncan K. and Klekowski R.Z. (1975) Parameters of an energy budget. International Biological Programme Handbook *24*, 97-147.

Enright C.T.; Newkirk G.F.; Craigie J.S. and Castell J.D. (1986a) Growth of juvenile *Ostrea edulis* L. fed *Chaetoceros gracilis* Schutt of varied chemical composition. J. Exp. Mar. Biol. Ecol. *96*, 15-26.

Enright C.T.; Newkirk G.F.; Craigie J.S. and Castell J.D. (1986b) Evaluation of phytoplankton as diets for juvenile *Ostrea edulis* L. J. Exp. Mar. Biol. *96*, 1-13.

Epifanio C.E. (1981) Phytoplankton and yeast as foods for juvenile bivalves: a review of research at the University of Delaware. Proc. 2^{nd} International Conference on Aquaculture Nutrition. Lewes/Rehobath Beach Delaware.

Epifanio C.E. and Ewart J. (1977) Maximum ration of four algal diets for the oyster *Crassostrea virginica* Gmelin. Aquaculture *11*, 13-29.
Epifanio C.E.; Srna R. and Pruder G. (1975) Mariculture of shellfish in controlled environments: a prognosis. Aquaculture *5*, 227-241.
Essink K. and Bos A.H. (1985) Growth of three bivalve molluscs transplanted along the axis of the Ems Estuary. Neth. J. Mar. Res. *19*, 45-51.
Estabrook G.F. and Dunham A.E (1976) Optimal diet as a function of absolute abundance, relative abundance and relative value of available prey. Amer. Natur. *110*, 401-413.
Famme P.; Riisgard H.U. and Jorgensen C.B. (1986) On direct measurement of pumping rates in the mussel *Mytilus edulis*. Mar. Biol. *92*, 323-327.
Flaws D.E. (1975) Aspects of the biology of mussels in the Cook Strait area. Ph.D. Thesis, Victoria University of Wellington.
Frechette M. and Bourget E. (1985a) Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. Can. J. Fish. Aquat. Sci. *42*, 1158-1165.
Frechette M. and Bourget E. (1985b) Food limited growth of *Mytilus edulis* in relation to the benthic boundary layer. Can. J. Fish. Aquat. Sci. *42*, 1166-1170.
Frechette M. and Bourget E. (1987) Significance of small-scale spatial heterogeneity in phytoplankton abundance for energy flow in *Mytilus edulis*. Mar. Biol. *94*, 231-240.
Gallager S.M. and Mann R. (1980) An apparatus for the measurement of grazing activity of filter feeders at constant food concentrations. Marine Biology Letters *1*, 341-349.
Garber K.J. (1983) Effect of fish size, meal size and dietary moisture on gastric evacuation of pelleted diets by yellow perch, *Perca flavescens*. Aquaculture *34*, 41-49.
Gerdes D. (1983) The Pacific oyster *Crassostrea gigas*. Part I. Feeding behaviour of larvae and adults. Aquaculture *31*, 195-219.
Gilles R. (1982) Osmoregulatory process in molluscs and crustaceans from media with fluctuating salinity regime. Bolm. Fisiol. Animal. Univ. S. Paulo *6*, 1-36.
Glynn P.W. (1973) Ecology of a Carribean coal reef. The *Porites* reef flat biotope: Part II. Plankton community with evidence for depletion. Mar. Biol. *22*, 1-21.
Gonzalez J.G. and Yevich P. (1976) Responses of an estuarine population of the blue mussel *Mytilus edulis* to heated water from a steam generating plant. Mar. Biol. *34*, 177-189.
Goodwin T.W. (1976) Chemistry and biochemistry of plant pigments. Volume 1. Academic Press, London. 870 pp.
Griffiths R.J. (1980) Filtration, respiration and assimilation in the black mussel *Choromytilus meridionalis*. Mar. Ecol. Prog. Ser. *3*, 63-70.
Griffiths C.L. and King J.A. (1979) Some relationships between size, food availability and energy balance in the ribbed mussel *Aulacomya ater*. Mar. Biol. *51*, 141-149.
Hargrave B.T. (1976) The central role of invertebrate faeces in sediment decomposition. Pp 301-322 *in* Proc. 17th Symposium of the British Ecological Society.
Harper A.E. (1967) Effects of dietary protein content and amino acid pattern on food intake and preference. Handbook of physiology, Sect. 6, Vol. *1*, 399-410.
Hawkins A.J.S.; Bayne B.L.; Mantoura R.F. and Llewellyn C.A. (1986) Chlorophyll degradation and absorption throughout the digestive system of the blue mussel *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol. *96*, 213-223.
Haury L.R.; McGowan J.A. and Wiebe P.H. (1977) Patterns and processes in the time-space scales of plankton distributions. Pp 277-328 *in* Steele J. (ed.). Spatial pattern in plankton communities. Plennum Press, London. 470 pp.
Heath R.A. (1982) Temporal variability in the waters of Pelorus Sound, South Island, New Zealand. N.Z. J. Mar. Freshwat. Res. *16*, 95-110.
Heisey D. and Porter K.G. (1977) The effect of ambient oxygen concentration on filtering and respiration of *Daphnia galeata mendotae* and *Daphnia magna*.

Limnol. Oceanogr. *22*, 839-845.
Helling G.R. and Baars M.A. (1985) Changes in the concentrations of chlorophyll and phaeopigment in grazing experiments. Hydrobiol. Bull. *19*, 41-48.
Herbert R.A. (1982) Nitrate dissimilation in marine and estuarine sediments. Pp 53-71 *in* Nedwell D.B. and Brown C.(eds.). Sediment microbiology. Academic Press, London. 234 pp.
Hickman R.W. (1979) Allometry and growth of the green-lipped mussel *Perna canaliculus* in New Zealand. Mar.Biol. *51*, 311-327.
Hickman R.W. and Illingworth J. (1980) Condition cycle of the green-lipped mussel *Perna canaliculus* in New Zealand. Mar. Biol. *60*, 27-38.
Hilbish T.J. (1986) Growth trajectories of shell and soft tissue in bivalves: seasonal variation in *Mytilus edulis*. J. exp. Mar. Biol. Ecol. *96*, 103-113.
Hildreth D.I. (1980) Bioseston production by *Mytilus edulis* and its effect in experimental systems. Mar. Biol. *55*, 309-315.
Hildreth D.I. and Crisp D.J. (1976) A corrected formula for calculation of filtration rate of bivalve molluscs in an experimental flowing system. J. Mar. Biol. Ass. U.K. *56*, 111-120.
Hrs-Brenko M. and Calabrese A. (1969) The combined effects of salinity and temperature on larvae of the mussel *Mytilus edulis*. Mar. Biol. *4*, 224-226.
Hughes R.N. (1980) Optimal forager theory in the marine context. Oceanogr. Mar. Biol. Ann. Rev. *18*, 423-481.
Hummel H. (1985a) Food intake of *Macoma balthica* (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. Neth. J. Sea Res. *19*, 52-76.
Hummel H. (1985b) An energy budget for a *Macoma balthica* (Mollusca) population living on a tidal flat in the Dutch Wadden Sea. Neth. J. Sea Res. *19*, 84-92.
Incze L.S.; Lutz R.A. and Watling L. (1980) Relationships between effects of environmental temperature and seston on growth and mortality of *Mytilus edulis* in a temperate northern estuary. Mar. Biol. *57*, 147-156.
Inoye D.W. and Waller G.D. (1984) Resposes of honey bees (*Apis mellifera*) to amino acid solutions mimicking floral nectars. Ecology *65*, 618-215.
Iverson R.L. (1977) Meroscale oceanic phytoplankton patchiness caused by hurricane effects on nutrient distribution in the gulf of Mexico. Pp 767-778 *in* Oceanic sound scattering prediction. Anderson N.R. and Bernard J.Z. (eds). Plennum Press, New York.
Johannes R.E. and Satomi M. (1966) Composition and nutritive value of faecal pellets of a marine crustacean. Limnol. Oceanogr. *11*, 191-197.
Kaspar H.F.; Gillespie P.A. and Boyer I.C. (1985) Effects of mussel aquaculture on the nitrogen cycle and benthic communities in the Kenepuru Sound, Marlborough Sounds, New Zealand. Mar. Biol. *85*, 127-136.
Kiorboe T.; Mohlenberg F. and Nohr O. (1980) Feeding, particle selection and carbon absorbtion in *Mytilus edulis* in different mixtures of algae and resuspended bottom material. Ophelia *19*, 193-205.
Kiorboe T.; Mohlenberg F. and Nohr O. (1981) Effect of suspended bottom material on growth and energetics in *Mytilus edulis*. Mar. Biol. *61*, 283-288.
Kiorboe T. and Mohlenberg F. (1981) Particle selection in suspension feeding bivalves. Mar. Ecol. Prog. Ser. *5*, 291-296.
Kirby-Smith W.W. (1972) Growth of the bay scallop: the influence of experimental water currents. J. Exp. Mar. Biol. Ecol. *8*, 7-18.
Kirby-Smith W.W. and Barber R.T. (1974) Suspension feeding aquaculture systems: effects of phytoplankton concentration and temperature on growth of the bay scallop. Aquaculture *3*, 135-145.
Kleppel G.S.; Pieper R.E. and Trager G. (1988) Variability in the gut contents of individual *Acartia tonsa* from waters off Southern California. Mar. Biol. *97*, 185-190.
Korringa P. (1976) Farming marine organisms low in the food chain. Elsevier, New York. 264 pp.

Landry M.R.; Hassett R.P. and Fagerness V. (1984) Effect of food acclimation on assimilation efficiency of *Calanus pacificus*. Limnol. Oceanogr. *29*, 361-364.
Lauder G.A. (1987) Coastal landforms and sediments of the Marlborough Sounds. Ph.D. Thesis, University of Canterbury, New Zealand.
Lehman J.T. (1976) The filter-feeder as an optimal forager and the predicted shapes of feeding curves. Limnol. Oceanogr. *21*, 501-516.
Leonard A.B.; Strickler J.R. and Holland N.D. (1988) Effects of current speed on filtration during suspension feeding in *Oligometra serripinna* (Echinodermata, Crinoidea). Mar. Biol. *97*, 111-125.
Levinton J. (1972) Stability and trophic structure in deposit-feeding and suspension-feeding communities. Amer. Nat. *106*, 472-486.
Loo L. and Rosenberg R. (1983) *Mytilus edulis* culture: growth and production in western Sweden. Aquaculture *35*, 137-150.
Lorenzen C.J. (1967) Determinations of chlorophyll and phaeopigments; spectrophotometric equations. Limnol. Oceanogr. *12*, 343-346.
Lutz R.A. (1980) Mussel culture and harvest: a north American perspective. Developments in Aquaculture and Fisheries Science *7*, 350 p.
Marine Farming Act (1971) The statutes of New Zealand 1971 *(1)*, 412-455.
Mackenzie A.L.; Kaspar H.F. and Gillespie P.A. (1986) Some observations on phytoplankton species composition, biomass, and productivity in Keneperu Sound, New Zealand, 1982-3. N.Z. J. Mar. Freshwat. Res. *20*, 397-405.
Mahin D.T. and Lofberg R.T. (1970) Determination of several isotopes in tissue by wet oxidation. Pp 212-221 *in* The current status of liquid scintillation counting. Bransome E.D. (ed.). Grune and Stratton, New York.
Mallet A.L. and Carver C.E.A. Coffen S.S. and Freeman K.R. (1987) Winter growth of the blue mussel *Mytilus edulis* L.: importance of stock and site. J. Exp. Mar. Biol. Ecol. *108*, 217-228.
Malouf R.E. and Breese W.P. (1977) Seasonal changes in the effects of temperature and water flow rate on the growth of juvenile Pacific oysters *Crassostrea gigas* (Thunberg). Aquaculture *12*, 1-13.
Mathers N.F. (1973) Carbohydrate digestion in *Ostrea edulis* L. Proc. malac. Soc. Lond. *40*, 359-367.
Maung Myint U. and Tyler P.A. (1982) Effects of temperature, nutritive and metal stressors on the reproductive biology of *Mytilus edulis*. Mar. Biol. *67*, 209-223.
Mohlenberg F. and Kiorboe T. (1981) Growth and energetics in *Spisula truncata* (Da Costa) and the effect of suspended bottom material. Ophelia *20*, 79-90.
Morales C.E. (1987) Carbon and nitrogen content of copepod faecal pellets: effects of food concentration and feeding behaviour. Mar. Ecol. Prog. Ser. *36*, 107-114.
Morton J. and Miller M. (1973) The New Zealand sea shore. Auckland, Collins. 653p.
Navarro J.M. and Winter J.E. (1982) Ingestion rate, assimilation efficiency and energy balance in *Mytilus chiliensis* in relation to body size and different algal concentrations. Mar. Biol. *67*, 255-266.
Nell J.A. and Wisely B. (1984) Experimental feeding of Sydney rock oysters (*Saccostrea commercialis*). III. Food concentration and fattening proceedures. Aquaculture *37*, 197-208.
Newell R.I.E. (1979) Biology of intertidal animals. Marine ecological surveys Ltd., Faversham, Kent, U.K. 781 pp.
Newell R.I.E. (1981) Molluscan bioenergetics - a synopsis. Pp 252-271 *in* Proc. 2nd International Conference on aquaculture nutrition. Lewes/Rehoboth Beach, Delaware.
Newell R.I.E. and Thompson R.J. (1984) Reduced clearance rates associated with spawning in the mussel *Mytilus edulis* (L.) (Bivalvia, Mytilidae). Mar. Biol. Letters *5*, 21-33.
Nicholajsen H.; Mohlenberg F. and Kiorboe T. (1983) Algal grazing by the planktonic copepods *Centropages hamatus* and *Pseudocalanus* sp.: diurnal and seasonal variation during the spring phytoplankton bloom in the Oresund. Ophelia *22*, 15-31.

Nixon S.W.; Oviatt C.A. and Rogers C. (1971) Mass and metabolism of a mussel bed. Oecologia (Berl.) *8*, 21-30.

Ohman M.D. (1988) Sources of gut variability in measurements of copepod lipids and gut fluorescence in the California Current coastal zone. Mar. Ecol. Prog. Ser. *42*, 143-153.

Okamura B. (1987) Particle size and flow velocity induce an inferred switch in bryozoan suspension-feeding behaviour. Biol. Bull. *173*, 222-229.

Page H.M. and Hubbard D.M. (1987) Temporal and spatial patterns of growth in mussels *Mytilus edulis* on an offshore platform: relationships to water temperature and food availability. J. Exp. Mar. Biol. Ecol. *111*, 159-179.

Perez A. and Roman G. (1979) Study of the mussel and its epifauna in the floating mussel farms of the Arosa Estuary. II. Mussel growth, mortality and production. Bol. Inst. Espa. Oceano. *V*, 23-39. [Spanish].

Pipe R.K. and Moore M.N. (1985) Ultrastructural changes in the lysosomal-vascuolar system in digestive cells of *Mytilus edulis* as a response to increased salinity. Mar. Biol. *87*, 157-163.

Qasim S.Z.; Parulkar A.H. and Harkantra S.N. (1977) Aquaculture of green mussel *Mytilus viridis* L.: cultivation on ropes from floating rafts. Indian J. Mar. Sci. *6*, 15-25.

Rainer S.F. (1985) Population dynamics and production of the bivalve *Abra alba* and implications for fisheries production. Mar. Biol. *85*, 253-262.

Riisgard H.U. and Mohlenberg F. (1979) An improved automatic recording apparatus for determining the filtration rate in *Mytilus edulis* as a function of size and algal concentration. Mar. Biol. *52*, 61-67.

Riisgard H.U. and Poulsen E. (1981) Growth of *Mytilus edulis* in net bags transferred to different localities in a eutrophicated Danish fjord. Mar. Pollution Bull. *12*, 272-276.

Riisgard H.U. and Randlov A. (1981) Energy budgets, growth and filtration rates in *Mytilus edulis* at different algal concentrations. Mar. Biol. *61*, 227-234.

Robert R.; His E. and Dinet A. (1988) Combined effects of temperature and salinity on fed and starved larvae of the european flat oyster *Ostrea edulis*. Mar. Biol. *97*, 95-100.

Rodhouse P.G. (1978) Energy transformations by the oyster *Ostrea edulis* L. in a temperate estuary. J. Exp. Mar. Biol. Ecol. *34*, 1-22.

Rodhouse P.G.; Roden C.M. and Hensey M.P. (1984) Resource allocation in *Mytilus edulis* on the shore and in suspension culture. Mar. Biol. *84*, 27-37.

Rodhouse P.G.; Roden C.M. and Hensey M.P. (1985) Production of mussels, *Mytilus edulis*, in suspended culture and estimates of carbon and nitrogen flow: Killary Harbour, Ireland. J. Mar.Biol. Ass. U.K. *65*, 55-68.

Romberger H.P. and Epifanio C.E. (1981) Comparative effects of diets consisting of one or two algal species upon assimilation efficiencies and growth of juvenile oysters, *Crassostrea virginica* (Gmelin). Aquaculture *25*, 77-87.

Rosenberg R. and Loo L-O. (1983) Energy flow in a *Mytilus edulis* culture in western Sweden. Aquaculture *35*, 151-161.

Ross R.M. (1982a) Energetics of *Euphausia pacifica*. I. Effects of body carbon and nitrogen and temperature on measured and predicted production. Mar. Biol. *68*, 1-14.

Ross R.M. (1982b) Energetics of *Euphausia pacifica*. II. Complete carbon and nitrogen budgets at $8^{o}C$ and $12^{o}C$ throughout the life span. Mar. Biol. *68*, 15-23.

Schiemer F. (1985) Bioenergetic niche differentiation of aquatic invertebrates. Verh. int. Verein. theor. angew. Limnol. *22*, 3014-3018.

Schoener T.W. (1971) Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2, 369-404.

Schulte E.H. (1975) Influence of algal concentration and temperature on the filtration rate of *Mytilus edulis*. Mar. Biol. *30*, 331-341.

Schwind P. (1977) Practical shellfish farming. International Marine Publishing Co., Camden, Maine.

Seed R. (1976) Ecology. Pp 13-66 *in* Marine mussels: their ecology and physiology.

Bayne B.L. (ed.). Cambridge University Press, London.
Shuman F.R. and Lorenzen C.J. (1975) Quantitative degradation of chlorophyll by a marine herbivore. Limnol. Oceanogr. *20*, 580-586.
Shumway S.E. and Newell R.C. (1984) Energy resource allocation in *Mulinia lateralis* (Say), an opportunistic bivalve from shallow water sediments. Ophelia *23*, 101-118.
Sindermann C.J. (1977) Disease diagnosis and control in north American marine aquaculture. Dev. Aquaculture Fish. Sci. *6*. 329 p.
Sivalingham P.M. (1977) Aquaculture of the green mussel, *Mytilus viridis* Linnaeus, in Malaysia. Aquaculture *11*, 297-312.
Smith C.H. (1986) A contribution to the geographical interpretation of biological change. Acta biotheoretica *35*, 229-278.
Sokal R.R. and Rohlf F.J. (1981) Biometry. 2nd edition. Freeman and Co, San Fransisco.
Snedecor G.W. and Cochran W.G. (1980) Statistical methods. 7th Edition. Iowa University Press, Ames, Iowa. 507 pp.
Sprung M. (1984a) Physiological energetics of mussel larvae (*Mytilus edulis*). I. Shell growth and biomass. Mar. Ecol. Prog. Ser. *17*, 283-293.
Sprung M. (1984b) Physiological energetics of mussel larvae (*Mytilus edulis*). II. Food uptake. Mar. Ecol. Prog. Ser. *17*, 295-305.
Sprung M. (1984c) Physiological energetics of mussel larvae (*Mytilus edulis*). IV. Efficiencies. Mar. Ecol. Prog. Ser. *18*, 179-186.
Sprung M. (1985) Experiments on nutritional stress in the larvae of the mussel *Mytilus edulis*. Pp 567-576 *in* Marine biology of polar regions and effects of stress on marine organisms. Gray J.S. and Christiansen M.E. (eds.). J. Wiley and Sons, London.
Stemberger R.S. (1986) The effect of food deprivation, prey density and volume on clearance rates and ingestion rates of *Diacyclops thomasi*. J. Plankton Res. *8* (2), 243-251.
Strickland J.D.H. and Parsons T.R. (1968) A practical handbook of seawater analysis. Fish Res. Bd. Can. Bull. *167*.
Stromgren T. and Cary C. (1984) Growth in length of *Mytilus edulis* L. fed on different algal diets. J. Exp. Mar. Biol. Ecol. *76*, 23-34.
Sullivan J.A. (1978) Fundamentals of fluid dynamics. Reston Publishing Co., Reston, Virginia. 275 pp.
Theede H. (1963) Experimentelle untersuchungen uber die filtrations leistung der miesmuschel *Mytilus edulis* L. Kieler Meeresforschungen *21*, 153-66.
Theisen B.F. (1977) Feeding rate of *Mytilus edulis* L. (Bivalvia) from different parts of Danish waters of different turbidity. Ophelia *16*, 221-232.
Thompson J.D (1981) Climate, upwelling and biological productivity: some primary relationships. Advances in Environmental Science and Technology *11*, 13-34.
Thompson J.K. and Nichols F.H. (1988) Food availability controls seasonal cycles of growth in *Macoma balthica* (L.) in San Francisco Bay, California. J. Exp. Mar. Biol. Ecol. *116*, 43-61.
Thompson R.J. (1984) The reproductive cycle and physiological ecology of the mussel *Mytilus edulis* in a subarctic, non-estuarine environment. Mar. Biol. *79*, 277-288.
Thompson R.J. and Bayne B.L. (1974) Some relationships between growth, metabolism and food in the mussel *Mytilus edulis*. Mar. Biol. *27*, 317-326.
Tortell P. (1976) An investigation into the settling behaviour of mussels and the hydrology of a selected area with a view to farming the shellfish. Ph.D. Thesis, Victoria University of Wellington.
Vahl O. (1979) An hypothesis on the control of food intake in fish. Aquaculture *17*, 221-229.
Walne P.R. (1972) The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves. J. Mar. Biol. Ass. U.K. *52*, 345-374.
Walz N. (1978) The energy balance of the freshwater mussel *Dreissena polymorpha*

Pallas in laboratory experiments and in Lake Constance. I. Pattern of activity, feeding and assimilation efficiency. Arch. Hydrobiol./Suppl. *55*, 83-105.
Wang R. and Conover R.J. (1986) Dynamics of gut pigment in the copepod *Temora longicornis* and the determination of *in situ* grazing rates. Limnol. Oceanogr. *31*, 867-877.
Weeber B. (1987) Aquacultural developments in 1986. Catch *14* (7), 5.
Weinberg J.R. (1985) Factors regulating population dynamics of the marine bivalve *Gemma gemma*: intraspecific competition and salinity. Mar. Biol. *86*, 173-182.
Welschmeyer N.A. and Lorenzen C.J. (1985) Role of herbivory in controlling phytoplankton abundance: annual pigment budget for a temperate marine fjord. Mar. Biol. *90*, 75-86.
Widdows J. (1973) The effects of temperature on the metabolism and activity of *Mytilus edulis*. Neth. J. Sea Res. *7*, 387-398.
Widdows J. (1978a) Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. J. Mar. Biol. Ass. U.K. *58*, 109-124.
Widdows J. (1978b) Physiological indices of stress in *Mytilus edulis*. J. Mar. Biol. Ass. U.K. *58*, 125-142.
Widdows J. (1985) The effects of fluctuating and abrupt changes in salinity on the performance of *Mytilus edulis*. Pp 555-566 *in* Marine biology of polar regions and effects of stress on marine organisms. Gray J.S. and Christiansen M. (eds.). J. Wiley and sons, London.
Widdows J.; Fieth P. and Worral C.M. (1979) Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. Mar. Biol. *50*, 195-207.
Widdows J. and Shick J.M. (1985) Physiological responses of *Mytilus edulis* and *Cardium edule* to aerial exposure. Mar. Biol. 85, 217-232.
Wildish D.J.; Kristmanson D.D.; Hoar R.L.; DeCoste A.M.; McCormick S.D. and White A.W. (1987) Giant scallop feeding and growth responses to flow. J. Exp. Mar. Biol. Ecol. *113*, 207-220.
Wildish D.J. and Kristmanson D.D. (1979) Tidal energy and sublittoral macrobenthic animals in estuaries. J. Fish. Res. Bd. Can. *36*, 1197-1206.
Wildish D.J. and Kristmanson D.D. (1988) Growth responses of giant scallops to periodicity of flow. Mar. Ecol. Prog. Ser. *42*, 163-169.
Wilkinson V. (1983) Chlorophyll a analysis - guidelines and procedures for extraction, measurement and calculation of chlorophyll *a* concentration. Unpublished report 27/T/62: DMFS, DSIR, PO Box 415, Taupo, New Zealand.
Wilson J.H. (1983) Retention efficiency and pumping rate of *Ostrea edulis* in suspensions of *Isochrysis galbana*. Mar. Ecol. Prog. Ser. *12*, 51-58.
Wilson J.H. and Seed R. (1974) Laboratory experiments on pumping and filtration in *Mytilus edulis* L. using suspensions of colloidal graphite. Irish Fish. Invest. Ser. B *14*, 3-20.
Windell J.T. (1978) Estimating food consumption rates of fish populations. International Biological Programme Handbook *3*, 227-253.
Windell J.T. and Bowen S.H. (1978) Methods for study of fish diets based on analysis of gut contents. International Biological Programme Handbook *3*, 219-226.
Winter J.E. (1969) Uber den einflub der nahrungkonzentration und anderer faktoren auf filtrierleistung und nahrungsausnutzung der muscheln *Arctica islandica* und *Modiolus modiolus*. Mar. Biol. *4*, 87-135.
Winter J.E. (1973) The filtration rate of *Mytilus edulis* and its dependance on algal concentration, measured by a continuous automatic apparatus. Mar. Biol. *22*, 317-328.
Winter J.E. (1978a) A review on the knowledge of suspension feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. Aquaculture *13*, 1-33.
Winter J.E. (1978b) A critical review on some aspects of filter feeding in lamellibranchiate bivalves. Haliotis, Paris *7*, 71-87.

Appendix 1. Data used to derive the regression models given in Section 2.2. Brief descriptions of all codes and units are given at the end of the table. Additional information on analytical methods is given in Section 2.1.

SITE	DATE	TEMP	SALT	CHLO	CARB	LENG	MDWT	MCON	DEN	P	FCHL	FRC	CING	AEC	CU
1	041083	13.4	30.5	1.67	2.72	50.4	1.64	12.0	300	2	11.3	1.9	0.12	86	0.111
1	041083	13.4	30.5	1.67	2.72	96.1	5.75	8.4	400	4	14.1	2.4	0.16	78	0.126
2	031083	13.6	29.8	2.04	3.24	54.3	1.08	9.5	280	2	11.4	1.7	0.13	93	0.127
2	031083	13.6	29.8	2.04	3.24	73.2	2.08	8.5	300	3	19.8	3.0	0.23	75	0.176
3	051083	12.6	31.0	2.55	2.58	50.4	0.65	8.0	250	2	6.1	0.5	0.03	85	0.027
3	051083	12.6	31.0	2.55	2.58	97.4	4.29	8.6	450	4	61.8	5.1	0.32	80	0.258
411	061083	12.2	32.9	0.69	1.84	79.8	3.76	12.0	290	2	15.2	3.8	0.17	84	0.145
421	061083	12.2	32.9	0.69	1.84	53.7	1.34	12.5	350	2	4.7	1.2	0.05	83	0.044
421	061083	12.2	32.9	0.69	1.84	82.1	4.50	12.4	300	3	13.7	3.5	0.15	71	0.110
422	061083	12.2	32.9	0.65	1.71	81.6	3.25	7.7	200	2	11.6	3.1	0.12	56	0.073
423	061083	12.2	32.9	0.62	1.66	84.5	4.49	12.4	350	2	19.3	5.5	0.21	84	0.185
431	061083	12.2	32.9	0.69	1.84	85.9	3.82	11.8	350	3	17.7	4.5	0.20	72	0.145
5	071083	12.2	34.1	0.92	1.28	50.7	0.86	10.2	340	2	4.5	0.8	0.02	88	0.023
5	071083	12.2	34.1	0.92	1.28	115.	5.20	7.7	280	2	67.4	12.	0.39	71	0.284
413	081183	14.5	30.2	1.12		84.7	4.20	12.4	300	2	16.8	5.7			
421	081183	14.5	30.2	1.17		85.5	4.02	12.3	320	3	40.9	13.			
422	081183	14.5	30.2	1.32		86.5	4.39	12.6	120	1	63.3	18.			
423	081183	14.5	30.2	0.79		44.9	0.62	7.4	350	2	9.4	4.6			
423	081183	14.5	30.2	0.79		94.3	5.39	12.2	100	1	28.2	13.			
433	081183	14.5	30.5	0.85		61.9	1.28	9.4	350	3	17.4	7.9			
1	121283	16.6	29.2	1.50		74.2	2.13	10.1	290	2	17.6	5.5			
1	121283	16.6	29.2	1.50		112.	7.75	11.1	400	4	26.5	8.4			
2	121283	16.8	29.5	1.75		55.3	1.07	10.0	280	2	15.2	4.1			
2	121283	16.8	29.5	1.75		114.	6.55	10.0	300	3	26.5	7.2			
3	121283	16.0	20.1	0.99		82.7	3.00	10.4	250	2	9.5	4.4			
3	121283	16.0	20.1	0.99		145.	13.6	9.9	450	5	21.5	10.			
413	101283	15.2	33.1	0.80		89.0	3.15	7.1	320	2	48.9	26.			
421	101283	15.2	33.7	1.21		95.8	4.13	9.6	300	2	59.7	21.			
422	101283	15.2	33.7	1.14		90.7	3.81	9.6	340	2	51.4	19.			
423	101283	15.2	33.7	1.29		50.8	1.49	9.8	400	2	13.5	4.4			
423	101283	15.2	33.7	1.29		92.4	3.87	9.5	250	2	55.2	18.			
433	101283	15.1	34.5	0.91		87.5	3.15	9.8	300	2	55.0	25.			
423	121283	16.7	19.2	0.34		90.3	3.16	8.3	350	2	5.5	7.7			
5	121283	15.7	31.6	0.94		51.1	0.50	6.9	370	2	11.7	5.6			
5	121283	15.7	31.6	0.94		73.1	1.50	7.3	280	2	26.1	12.			
411	080184	16.1	31.3	0.32		89.5	3.57	10.6	320	2	6.7	9.7			
421	080184	16.0	32.3	0.35		41.2	0.32	7.1	205	2	3.9	5.1			
421	080184	16.0	32.3	0.35		99.8	5.25	11.4	200	2	15.2	20.			
422	080184	16.0	32.3	0.33		92.0	3.89	10.6	290	4	9.4	13.			
423	080184	16.0	32.3	0.35		92.0	3.66	9.7	260	3	5.4	7.1			
431	080184	15.9	33.1	0.35		111.	6.53	11.2	175	2	13.6	17.			
1	110284	18.2	32.7	1.25		80.3	2.30	8.6	540	4	16.8	6.6			
2	110284	17.9	33.2	1.01		77.8	2.21	6.7	340	2	21.7	10.			
2	110284	17.9	33.2	1.01		119.	9.32	11.0	210	2	38.6	18.			
3	120284	17.2	33.7	1.05		86.6	3.36	10.1	230	2	21.1	9.7			
411	120284	17.2	33.7	0.68		73.0	1.43	7.4	330	2	27.4	19.			
421	120284	17.2	34.1	0.89		51.5	0.52	6.5	330	2	11.0	6.0			
421	120284	17.2	34.1	0.89		101.	2.95	7.5	350	3	46.6	25.			
422	120284	17.2	34.1	0.76		97.0	3.27	8.2	330	3	25.9	16.			
423	120284	17.2	34.1	0.91		101.	3.24	8.2	410	4	36.2	19.			
431	120284	17.2	34.2	0.82		93.4	2.73	7.7	240	2	47.9	28.			
5	130284	16.8	34.2	0.73		48.9	0.56	8.8	106	3	19.5	12.			
5	130284	16.8	34.2	0.73		82.0	2.14	7.7	230	2	42.1	27.			

SITE	DATE	TEMP	SALT	CHLO	CARB	LENG	MDWT	MCON	DEN	P	FCHL	FRC	CING	AEC	CU
411	090384	18.7	27.9	1.34	1.07	79.8	1.58	7.1	300	2	34.5	12.	0.33	62	0.207
421	090384	18.7	27.3	1.17	1.17	58.5	0.64	6.5	200	1	17.7	7.5	0.21	64	0.136
421	090384	18.7	27.3	1.17	1.17	102.	3.61	8.3	220	2	47.4	20.	0.56	75	0.426
422	090384	18.7	27.3	1.06	1.06	103.	3.67	7.8	275	2	41.4	19.	0.49	71	0.354
423	090384	18.7	27.3	1.04	1.04	101.	3.51	8.3	300	3	48.9	23.	0.58	77	0.455
431	090384	18.7	24.9	1.14	1.14	103.	3.78	8.5	220	2	39.8	17.	0.47	75	0.362
1	050484	18.0	32.6	3.15	2.88	41.1	0.26	6.7	840	4	17.6	2.7	0.19	86	0.166
1	050484	18.0	32.6	3.15	2.88	83.2	1.98	7.5	310	2	50.8	7.9	0.55	81	0.448
2	040484	17.6	32.1	2.34	2.36	29.4	0.13	6.5	740	2	8.1	1.7	0.09	80	0.077
2	040484	17.6	32.1	2.34	2.36	83.7	2.27	7.5	420	2	58.	12.	0.69	85	0.594
3	050484	17.5	32.6	2.34	2.69	101.	4.20	8.2	310	2	26.7	5.5	0.36	41	0.148
413	060484	17.2	33.8	2.18	2.97	84.7	3.34	7.2	320	2	50.6	11.	0.80	85	0.690
421	060484	17.2	32.8	2.28	3.10	84.7	2.75	9.5	320	3	20.6	4.4	0.32	67	0.222
422	060484	17.2	32.8	2.23	3.03	89.7	3.31	9.3	380	3	44.1	9.6	0.70	86	0.604
423	060484	17.2	32.8	2.59	3.52	63.7	1.40	6.8	340	2	15.0	2.8	0.23	62	0.149
423	060484	17.2	32.8	2.59	3.52	92.9	3.70	9.3	350	3	23.7	4.4	0.37	76	0.288
433	060484	17.2	30.9	2.08	2.83	105.	5.76	10.4	320	3	43.5	10.	0.69	80	0.554
5	070484	16.9	34.3	1.61	2.17	36.6	0.24	5.2	450	2	18.3	5.4	0.28	87	0.249
5	070484	16.9	34.3	1.61	2.17	84.6	2.38	7.3	410	3	59.1	17.	0.92	88	0.817
411	080584	15.5	34.3	2.08	0.94	67.6	1.82	10.3	225	2	22.5	4.7	0.10	28	0.030
421	080584	15.5	31.4	1.41	0.93	75.5	6.57	10.8	125	2	73.0	22.	0.51	79	0.406
421	080584	15.5	31.4	1.41	0.93	111.	2.31	10.9	170	2	26.3	8.2	0.18	37	0.069
422	080584	15.5	31.4	1.16	0.76	74.8	2.07	10.0	230	2	26.1	9.9	0.18	20	0.037
423	080584	15.5	31.4	1.22	0.81	78.5	2.51	10.8	200	2	36.4	13.	0.25	61	0.158
431	080584	15.5	32.7	1.57	1.27	84.2	3.31	10.8	100	1	34.5	9.7	0.29	74	0.222
1	070684	11.5	34.1	2.36	2.35	60.2	1.13	9.0	530	3	24.4	1.2	0.06	78	0.054
1	070684	11.5	34.1	2.36	2.35	93.8	3.04	7.4	240	2	58.9	2.9	0.16	82	0.138
2	060684	12.1	32.8	1.29	1.88	48.0	0.47	6.9	470	2	15.9	2.0	0.09	74	0.069
2	060684	12.1	32.8	1.29	1.88	96.8	5.46	8.4	240	2	84.6	11.	0.49	84	0.418
3	080684	12.8	33.5	1.13	2.14	110.	5.40	9.0	210	3	81.6	16.	0.86	88	0.771
411	090684	12.1	33.7	1.22	2.00	82.0	3.18	10.1	310	2	42.7	5.8	0.28	89	0.251
421	090684	12.3	29.4	1.39	2.28	54.6	0.86	8.2	290	2	9.8	1.3	0.07	80	0.057
421	090684	12.3	29.4	1.39	2.28	80.1	2.52	9.6	310	2	57.7	7.7	0.42	92	0.392
422	090684	12.3	29.4	1.31	2.14	82.6	2.75	9.4	340	2	48.6	6.8	0.35	90	0.319
423	090684	12.3	29.4	1.22	2.01	87.8	3.79	10.9	340	2	45.1	6.8	0.33	88	0.292
431	090684	11.9	27.1	1.57	2.57	79.0	2.69	10.0	320	2	33.3	3.1	0.19	84	0.167
5	100684	13.4	34.6	0.91	2.03	47.1	0.32	6.2	450	2	12.1	3.8	0.18	78	0.149
5	100684	13.4	34.6	0.91	2.03	103.	4.66	8.7	320	2	61.4	19.	0.96	86	0.836
421	100784	11.7	29.2	2.54	1.40	58.6	1.23	9.6	240	2	27.0	1.4	0.04	69	0.033
421	100784	11.7	29.2	2.54	1.40	86.8	3.26	10.4	250	2	51.4	2.7	0.09	72	0.066
422	100784	11.7	29.2	2.51	1.38	85.4	3.15	10.1	230	2	66.2	3.5	0.11	75	0.088
423	100784	11.7	29.2	2.54	1.40	90.8	3.51	9.6	200	2	61.9	3.2	0.11	76	0.084
431	100784	11.6	29.1	2.34	1.42	82.9	2.83	9.1	260	2	51.3	2.7	0.09	72	0.068
1	050884	11.0	30.3	1.57	1.75	43.1	0.60	10.6	560	2	41.6	2.3	0.09	84	0.082
1	050884	11.0	30.3	1.57	1.75	91.4	2.24	6.2	370	4	81.8	4.5	0.19	89	0.171
2	040884	11.4	30.2	1.18	1.62	54.3	0.81	7.8	290	2	47.3	4.5	0.17	95	0.167
2	040884	11.4	30.2	1.18	1.62	91.7	2.40	5.8	250	3	107.1	10.	0.39	91	0.365
421	070884	11.3	28.7	2.69	1.92	91.4	3.64	9.8	250	2	57.7	2.2	0.10	80	0.084
422	070884	11.3	28.7	2.75	1.97	87.7	3.44	10.2	250	2	53.2	2.0	0.09	82	0.080
423	070884	11.3	28.7	3.40	2.43	69.5	1.43	7.5	210	2	30.4	0.9	0.05	75	0.041
423	070884	11.3	28.7	3.40	2.43	93.1	4.33	10.7	270	2	59.1	1.8	0.10	82	0.088
433	070884	11.4	28.6	3.60	2.57	88.7	3.98	10.6	270	2	58.4	1.8	0.11	85	0.096
5	080884	11.9	34.0	1.07	1.93	53.5	0.39	5.4	440	2	20.0	2.8	0.13	81	0.106
5	080884	11.9	34.0	1.07	1.93	96.7	1.86	4.8	280	2	76.9	10.	0.50	89	0.450

SITE	DATE	TEMP	SALT	CHLO	CARB	LENG	MDWT	MCON	DEN	P	FCHL	FRC	CING	AEC	CU
411	120984	12.7	30.8	1.96	1.19	95.6	5.08	11.1	180	2	10.6	1.2	0.03	6	0.002
421	120984	12.7	31.1	1.86	0.94	61.3	1.56	10.9	150	1	15.9	1.9	0.04	0	0.000
421	120984	12.7	31.1	1.86	0.94	96.6	5.30	12.3	180	2	48.9	5.8	0.13	52	0.069
422	120984	12.7	31.1	1.77	0.87	94.9	4.55	11.6	180	2	27.9	3.5	0.07	35	0.026
423	120984	12.7	31.1	1.77	0.86	97.3	4.91	10.9	170	2	31.2	3.9	0.08	49	0.040
431	120984	12.7	28.7	2.23	1.02	89.9	4.36	11.6	210	2	32.8	3.2	0.08	41	0.033

SITE: coded as n1,n2,n3 where n1=embayment (1=Mills Bay, 2=Schnapper Pt, 3= Four Fathom Bay, 4=Crail Bay, 5=Richmond), n2=farm position (1=northern, 2= central, 3=southern) and n3=site in farm (1=northern, 2=central, 3=southern). DATE: coded as ddmmyy where dd=day, mm=month, yy=year. TEMP: temperature (°C). SALT: salinity (ppt). CHLO: chlorophyll a concentration (ug l^{-1}). CARB: Particulate Organic Matter (mg l^{-1}). LENG: mussel shell length (mm). MDWT: tissue dry weight (g ind^{-1}). MCON: condition index. DEN: growth density (n m^{-1}). P: packing index (1=sparse, 2=low density, 3=well distributed, 4=dense with little additional room for growth, 5=mussels forming clumps on rope). FCHL: chloropigment content of mussel faeces (ug chlorophyll equivalent). FRC: Filtration rate (l h^{-1}). CING: Quantity of carbon ingested (gC d^{-1}). AEC: Assimilation efficiency (%). CU: Carbon uptake (gC d^{-1}).